GENETICS

AN INTRODUCTION TO THE STUDY OF HEREDITY

BY

HERBERT EUGENE WALTER
PROFESSOR OF BIOLOGY, BROWN UNIVERSITY

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THIS VOLUME

IS AFFECTIONATELY DEDICATED

TO THE MEMORY OF

MY MOTHER

PREFACE TO THE REVISED EDITION

NEARLY ten years have passed since this book first appeared. The biological Rip van Winkle of today who, awaking after a decade of somnolence, gazes again upon the genetic village of Falling Waters, will indeed need to rub his astonished eyes at the changed scene that now spreads out before him. Many old familiar landmarks, such as "unit characters" and "dominance," show signs of dilapidation, while strange children, shouting a medley of outlandish words, "linkage," "tetraploidy," and "non-disjunction," for example, are playing new games on the village green.

Although the remarkable advances in this field of science are well treated in considerable detail by several recent text-books, notably those of Castle, Morgan, Conklin, and Babcock and Clausen, perhaps there still remains the original need for a more elementary presentation of the salient points of genetics, not only for the interested but confused layman, but also for the initiation of the prospective student who is attracted to the study of heredity.

To perform this service is the ambitious object of the present revision.

Three new chapters, XI, XII and XIII, have been added and the whole book has been thoroughly worked over and rearranged. Chapter XIII upon Sex Determination has practically been written by Professor S. I. Kornhauser of Denison University and the entire

manuscript critically read by Dr. J. W. Wilson of Brown University.

There are thirty-four new figures and diagrams which are either original or copied from acknowledged sources. Mr. C. J. Fish made the drawings for figures 22 and 32. The proof was read by my wife and by my niece, Miss Dorothy Walter.

I wish to acknowledge the help I have received from all of these sources as well as from many unnamed friends who have given valuable suggestions.

H. E. W.

La Jolla, Calif.,
March 18, 1922.

PREFACE TO THE FIRST EDITION

THE following pages had their origin in a course of lectures upon Heredity, given at Brown University during the winter of 1911-1912, which were amplified and repeated in part the following summer at Cold Spring Harbor, Long Island, before the biological summer school of the Brooklyn Institute of Arts and Sciences.

An attempt has been made to summarize for the intelligent, but uninitiated, reader some of the more recent phases of the questions of heredity which are at present agitating the biological world. It is hoped that this summary will not only be of interest to the general reader, but that it will also be of service in college courses dealing with evolution and heredity.

The subject of heredity concerns every one, but many of those who wish to become better informed regarding it are either too busily engaged or lack the opportunity to study the matter out for themselves. The recent literature in this field is already very large, with every indication that much more is about to follow, which is a further discouragement to non-technical readers.

It may not be a thankless task, therefore, out of the jargon of many tongues to raise a single voice which shall attempt to tell the tale of heredity. There may be a certain advantage in having as spokesman one who is not at present immersed in the arduous

technical investigations that are making the tale worth telling. The difficulties in understanding this complicated subject may possibly be realized better by one who is himself still struggling with them, than by the seasoned expert who has long since forgotten that such difficulties exist.

Among others I am particularly indebted to Dr. C. B. Davenport for many helpful suggestions, to my colleague, Professor A. D. Mead, for reading the manuscript critically, to Dr. S. I. Kornhauser who gave valuable aid in connection with the chapter on the Determination of Sex, and to my wife for assistance in final preparation for the press.

I wish to thank Professor H. S. Jennings and Dr. H. H. Goddard, who have given generous permission to copy certain diagrams, as well as The Outlook Company and The Macmillan Company for the use of figures 24 and 66, respectively.

The fact that not all the suggestions which were at various times offered by my kindly critics have been incorporated in the text, absolves them from responsibility for whatever remains.

H. E. W.

PROVIDENCE, R. I.,
September, 1912

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CHAPTER I

INTRODUCTION

1. The Idea of Species

The doctors have always disagreed regarding a definition of species. What determines the exclusive boundaries that shall isolate from their fellows any particular group of animals or plants has long been a mooted question, and still remains so.

The Linnæan concept of a species was that of an exclusive caste of individuals, inflexibly demarked, over whose high barriers no nondescript tramps would dare attempt to climb. When an entomologist of the old Linnæan school encountered an insect which did not conform to the morphological traditions of its fellows, the frequent fate of such a nonconformist was to perish under the boot-heel rather than to find sanctuary in the cabinet of the preserved. Since it was an exception, and a violator of the divine law of the fixity of species, it deserved to be annihilated! Those were hard days both for heretics and for variations.

The method of the older school of systematists

may be described as one which emphasized *differences* and put up barriers that should keep the unlike apart, at the same time allowing only "birds of a feather" to flock together. It was a brave and successful attempt to bring order out of chaos by classifying the living world, and it served its purpose well until Darwin's idea of half a century ago, that the origin of all species is from preceding species, put an entirely new face upon the whole matter. Organisms of different species were found to be *related to one another,* and even man could no longer escape acknowledging his poor animal relations. As a consequence, *likenesses rather than differences* thereafter claimed the most attention.

During the reconstruction of phylogenetic trees, which seized the imagination and became the principal business of post-Darwinian biologists, "connecting links," that is, the crotched sticks in the woodpile of organisms, which had hitherto been largely discarded, were most eagerly sought after. It was just these scraggly sticks, that were neither trunk nor limb-wood but combinations of both, which told the story of continuity and were indispensable in building up a reunited whole.

As the analysis of the living world gradually came to shift from species to individuals, it was shown that individuals may be regarded simply as aggregates of *unit characters* which may combine so variously that it becomes more and more difficult to maintain constant barriers of any kind between the groups of individuals arbitrarily called "species."

2. The Triangle of Life

Accordingly within a generation the center of biological interest gradually swung from the origin of species to the origin of the individual. The nineteenth century was Darwin's century. His monumental work "On the Origin of Species by Means of Natural Selection," which appeared in 1859, not only dominated the biological sciences but also influenced profoundly many other realms of thought, particularly those of philosophy and theology.

Now, in the first decades of the twentieth century, a particular emphasis is being laid upon the study of heredity. The interpretation of investigations along this line of research has been made possible through the cumulative discoveries of many things that were not known in Darwin's day. Trained students, patiently and persistently bending over improved microscopes, have untangled the mysteries of the cell, while an increasing host of investigators, inspired by the Austrian monk Mendel, have industriously devoted their energies to breeding animals and plants with an insight denied to breeders of preceding centuries.

The study of the origin of the individual, which has grown out of the more general consideration of the origin of species, forms the subject-matter of heredity, or, to use the more definitive word of Bateson, of *genetics*.

It is not with the individual as a whole that genetics is chiefly concerned, but rather with *characteristics* of the individual.

Three factors acting together determine the characteristics of an individual, namely, *environment*, *response*, and *heritage*, as expressed diagrammatically in Figure 1. It may be said that an individual is the result of the *interaction* of these three factors since he may be modified by changing any one of them. Although no one factor can possibly be omitted, the student of genetics places the emphasis upon heritage as the

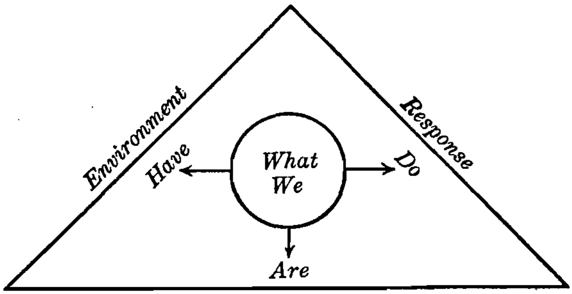


Fig. 1.—The triangle of life.

factor of greatest importance. Heritage, or "blood," expresses the innate equipment of the individual. It is what he actually *is* even before birth. It is his nature. It is what determines whether he shall be a beast or a man. Consequently in the diagram (Fig. 1), the triangle of life is represented as resting solidly upon the side marked "heritage" for its foundation.

Environment and response, although indispensable, are both factors which are subsequent and secondary. Environment is what the individual *has*, for example, housing, food, friends and enemies or surrounding aids which may help him and obstacles which he must

overcome. It is the particular world into which he comes, the measure of opportunity given to his particular heritage.

Response, on the other hand, represents what the individual *does* with his heritage and environment. It is what may be described as the training or educational factor. Lacking a suitable environment a good heritage may come to naught like good seed sown upon stony ground, but it is nevertheless true that the best environment cannot make up for defective heritage or develop wheat from tares.

The absence of sufficient response even when the environment is suitable and the endowment of inheritance is ample will result in an individual who falls short of his possibilities, while no amount of response or education can develop a man out of the heritage of a beast. Consequently the biologist holds that, although what an individual *has* and *does* is unquestionably of great importance, particularly to the individual himself, what he *is*, is in the long run far more important. Improved environment and training may better the generation already born. Improved blood will better every generation to come. The "triangle of life," when applied to man, shows that there are theoretically at least twenty-seven possible kinds of human beings as shown in Figure 2. Climbing up this "scale of success" is what makes life worth living. It is illuminating for any one to determine judiciously where he himself stands at present or to assign places mentally to various other people, historical and contemporary, in this scale.

The left-hand factor does not change throughout

	Heritage	Environment	Response
1.	A	A	A
2.	A	A	B
3.	A	A	C
4.	A	B	A
5.	A	B	B
6.	A	B	C
7.	A	C	A
8.	A	C	B
9.	A	C	C
10.	B	A	A
11.	B	A	B
12.	B	A	C
13.	B	B	A
14.	B	B	B
15.	B	B	C
16.	B	C	A
17.	B	C	B
18.	B	C	C
19.	C	A	A
20.	C	A	B
21.	C	A	C
22.	C	B	A
23.	C	B	B
24.	C	B	C
25.	C	C	A
26.	C	C	B
27.	C	C	C

FIG. 2.—The Scale of Success. A stands for high grade; B, for mediocrity; C, for low grade.

life but the other two may. The sociologist and the philanthropist are immediately concerned with the middle column; the educator and particularly the parent with the right-hand column; while the biologist puts faith in the left-hand column of heritage. For example, a child born ACC is more apt to reach the top than one born CCC. In selecting a mate it would be far wiser to marry ACC than CAA, since "blood will tell."

What, then, is this "blood" or heritage? Exactly what is meant by heredity?

3. A Definition of Heredity

The terms *heredity* and *inheritance* come to us from legal practice. We "inherit" the old homestead or our grandfather's clock. Moreover, as "heirs to all the ages" our heredity in-

cludes everything that goes to make up civilization, such as the arts, sciences, literature and traditions. With this kind of heredity we are not here concerned, for this is not what is meant by biological heredity.

Professor Castle, in his book on "Heredity in Relation to Evolution and Animal Breeding," has defined heredity as "organic resemblance based on descent." The son resembles his father because he is a "chip off the old block." It would be still nearer the truth to say that the son resembles his father because they are *both chips from the same block*, since the actual characters of parents are never transmitted to their offspring in the same way that real estate or personal property is passed on from one generation to another. When the son is said to have his father's hair and his mother's complexion it does not mean that paternal baldness and a vanishing maternal complexion are the inevitable consequences.

Biological inheritance is more comparable to the handing down from father to son of some valuable patent right or manufacturing plant by means of which the son, in due course of time, may develop an independent fortune of his own, resembling in character and extent the parental fortune similarly derived although not identical with it.

So it comes about that "organic resemblance" between father and son, as well as that which often appears between nephew and uncle or even more remote relatives, is due not to a direct entail of the characteristics in question, but to the fact that the characteristics are "based on descent" *from a common*

source. In other words, an "hereditary character" of any kind is not an entity or unit which is handed down from generation to generation, but is rather a *method of reaction* of the organism to the constellation of external environmental factors under which the organism lives.

To unravel the golden threads of inheritance which have bound us all together in the past, as well as to learn how to weave upon the loom of the future, not only those old patterns in plants and animals and men which have already proven worth while, but also to create new organic designs of an excellence hitherto impossible or undreamed of, is the inspiring task before the geneticist to-day.

4. The Maintenance of Life

So far as we know, every living thing on the earth to-day has arisen from some preceding form of life.

How the first spark of life began will probably always be a matter of pure speculation. Whether the beginnings of what is called life came through space from other worlds on meteoric wings, as Lord Kelvin has suggested; whether it was spontaneously generated on the spot out of lifeless components; or whether life itself was the original condition of matter, and the one thing that must be explained is not the origin of life but of the non-living, no one can say. Leaving aside the first speculation as untenable and the third as irrational, since it jars so sadly with what astronomers tell us of the probable

evolution of worlds, the theory of spontaneous generation seems to be the last resort to which to turn.

In prescientific days this idea of spontaneous generation presented no great difficulties to our imaginative and credulous ancestors. John Milton, with the assurance of an eye-witness, thus described the inorganic origin of a lion:—

> "The grassy clods now calved; now half appears
> The tawny lion, pawing to get free
> His hinder parts — then springs as broke from bonds,
> And rampant shakes his brindled mane."
> ("Paradise Lost," Book VII, line 543.)

Ovid also in his "Metamorphoses," not to mention a more familiar instance of special creation, easily succeeded in creating mankind from the humble stones tossed by the juggling hands of Deucalion and Pyrrha.

Although under former conditions on the earth it might have been possible for life to have originated spontaneously, and although it may yet be possible to produce life from inorganic materials in the laboratory or elsewhere, the exhaustive work of Pasteur, Tyndall and others effectually demonstrated a generation ago that to-day living matter always arises from preceding living matter and this conclusion is generally accepted as an axiom in genetics.

There are various methods of producing *more* life, given a nest-egg of living substance with which to start. Any organism, whether plant or animal, is continually transforming inorganic and dead material into living tissue. Through the process of repair, for example, an injury to a form as highly developed

even as man is frequently made good, if it is not too extensive and does not involve too highly specialized tissues, as, for example, in the case of a skin wound.

When the intake of non-living material is in excess of the outgo, growth results, with the consequence that more living substance is built up than existed before. Thus a fragment of a living sponge or a piece of a begonia leaf is each sufficient to restore a duplicate of the original organism.

A process similar to the repair of the begonia leaf is that employed so effectively in the great groups of the one-celled animals and plants, the Protozoa and Protophyta, by means of which their numbers are maintained. These one-celled organisms usually multiply by fission, that is, by division into halves, and each half grows to the size of the parent organism from which it sprang. When two daughter protozoans are thus formed, they are essentially orphans because they have no parents, alive or dead. The parental substance in such a process, along with the regulating power necessary to reorganization, goes over bodily into the next generation in the formation of the daughter-cells, leaving usually no remains whatever behind. In primitive forms of this description, continuous life is the natural order, and death, when it does occur, is, as Weismann has pointed out, accidental and quite outside the plan of nature.

In these cases, it is easy to see the reason for "organic resemblance" between successive generations. Parent and offspring are successive manifestations of the *same thing*, just as the begonia plant, restored

from a fragment of a begonia leaf, is simply an extension of the original plant.

Many modifications of the process of multiplication by fission occur, all of them, however, agreeing in the fundamental principle that the progeny resemble the parents because they are pieces of the parents.

Thus the "greening" apple maintains its individuality although coming from thousands of different trees, because all of these trees through the asexual process of grafting are continuations of the one original Rhode Island greening tree grown by Dr. Solomon Drowne in the town of Foster, nearly a century ago. Western navel oranges all come, directly or indirectly, from parts of one tree found near Bahia in Brazil.

Again, certain fresh-water sponges and bryozoans, quite unlike most of their marine relatives, keep a foothold from year to year within their particular shallow fresh-water habitats by isolating well protected fragments of themselves in the form of *gemmules* and *statoblasts*. These structures may drop to the muddy bottom and live in a dormant condition throughout the icy winter when it would not be possible for the entire organism to survive near the surface.

In order to meet the conditions imposed by winter, however, these fragments have become so modified as temporarily to lose their likeness to the parent generation, although readily regaining that likeness when springtime brings the opportunity. The unity of two succeeding generations, notwithstanding that it may be interrupted by the temporary interposition of something apparently different in the form of gemmules

or statoblasts, is thus essentially maintained. The bryozoan colonies of two successive seasons in a fresh-water pond may be regarded as parts of the same identical colony, since they present an "organic resemblance based on descent," although the sole representatives of the parent colony during midwinter may be the sparks of life locked up within the statoblasts buried in the mud.

Similarly, the asexual spores of many plants, such as molds, mosses and ferns, may be regarded as gemmules reduced to the lowest terms, namely, to single cells. As in the preceding cases so in this instance the resemblance of the offspring which may arise from these spores, to the parents which produced them, is due to the essential material identity of two generations.

These illustrations of heredity in its simplest manifestations give the key to "organic resemblance" higher up in the scale. Sexual reproduction is no less plainly the direct continuation of life though in this instance *two* sporelike fragments out of one generation contribute to form the new individual of the next generation instead of *one* fragment. In all cases there is a *material continuity between succeeding generations.* Offspring become thus an extension of a single parent, or of two parents, while heredity is simply "organic resemblance based on descent."

5. Somatoplasm and Germplasm

In forms that reproduce sexually there occurs a differentiation of the body substance into what Weismann terms *somatoplasm* and *germplasm.*

Somatoplasm includes the body tissues, that is, the bulk of the individual, which is fated in the course of events to complete a life-cycle and die. Germplasm, on the contrary, is the immortal fragment freighted with the power to duplicate the whole organism and which, barring accident, is destined to live on and give rise to new individuals.

Germplasm thus carries potencies for developing both germplasm and somatoplasm, while somatoplasm, according to this conception, has only the power to repair itself but not to reproduce a new individual. Moreover, germplasm is not freshly formed in each generation, neither does it arise anew when the individual reaches sexual maturity, as it appears to do, but it is a continuous substance present from the beginning. Although this theory of the *continuity of the germplasm* has been actually demonstrated in comparatively few instances, all the facts we know concerning the behavior of the germinal substance are consistent with it.

The phrase "life everlasting" is not confined, therefore, to the vocabulary of the theologian, and potential immortality is more than a mystical hope of believing humanity. They are based upon demonstrable biological facts.

In many of the Protozoa the entire organism is possibly comparable to germplasm, but in all forms of life that are compounded of several cells the germplasm is probably set aside early in the development of the individual, and this remains undifferentiated, or in reserve, like a savings-bank account put by for a rainy day, while the somatoplasm is expended in the imme-

diate demands of the tissues that make up the individual. In one instance at least, that of the nematode worm *Ascaris*, according to Boveri, this splitting off or isolation of the germplasm occurs as early in the cleavage of the fertilized egg as the sixteen-cell stage, when fifteen of the cells go to form the somatoplasm and the sixteenth is set aside as germplasm.

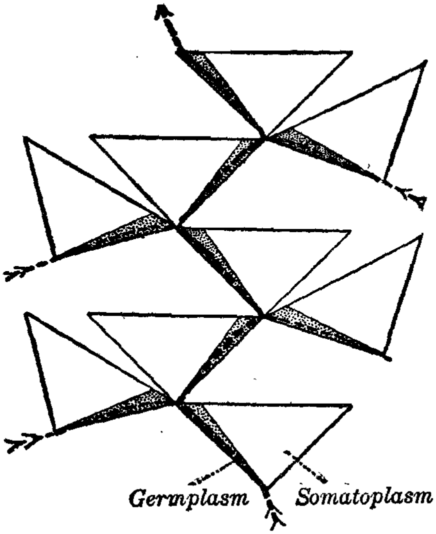


FIG. 3.—Scheme to illustrate *the continuity of the germplasm.* Each triangle represents an individual made up of *germplasm* (dotted) and *somatoplasm* (undotted). The beginning of the life cycle of each individual is represented at the apex of the triangle where germplasm and somatoplasm are both present. As the individual develops each of these component parts increases. In sexual reproduction the germplasms of two individuals unite into a common stream to which the somatoplasm makes no contribution. The continuity of the germplasm is shown by the heavy broken line into which run collateral contributions from successive sexual reproductions.

Thus there results a continuous stream of germplasm, receiving contributions from other germplasmal streams at the time of sexual reproduction, as shown diagrammatically in Figure 3, in which individuals are represented by tri-

angles. From this continuous stream of germplasm there split off at successive intervals complexes of somatoplasm, or "individuals," which go so far on the road of specialization into tissues that the power to be "born again" is lost, and so after a time they die, while the germplasm, held in reserve, lives on.

This is what is meant by saying that a father and son owe their mutual resemblance to the fact that they are chips off the same block rather than by saying that the son is a chip off the paternal block. Both somatoplasms are developments *at different intervals* from the same continuous stream of germplasm instead of one somatoplasm derived from a preceding one. As a matter of fact the germplasm from which the son arises is modified by the addition of a maternal contribution, so that father and son in reality hold the same relation to each other that half-brothers do.

So far as his body or his somatoplasm is concerned, the son is younger than his father but at the same time he is older than his father in his germplasm, because this continuous line of germinal potentiality has a generation longer span in him than in his parents.

From the point of view of genetics, then, the real mission of the somatoplasm, which is so marvelously differentiated into all the various forms that we call animals and plants, is simply to serve as a temporary domicile for the immortal germplasm. Thus the parent becomes as it were the "trustee of the germplasm," but not the producer of the offspring, for the soma is after all only the mechanism through which a fertilized egg produces in due time another fertilized egg.

In the light of these preliminary explanations it is plain that the hopeful point of attack in the science of genetics must inevitably be the germplasm which is the source, or point of departure, in the formation of each new individual, rather than the somatoplasm, which represents the end stages of the hereditary processes.

This has not been the method of study in the past. The resemblances of the visible father and son have usually been traced instead of the character of their unseen germplasms. By following this old method, investigators have often been misled because the visible or apparent is not always the true index of what lies behind it. A gray and a white rabbit, for example, may produce some offspring that are entirely black or two white-flowering sweet peas when crossed may sometimes produce purple blossoms. Consequently it is a great fallacy to affirm that always in heredity "like produces like," since the opposite is quite often the case.

The new heredity, embodied in the science of genetics, attempts to go deeper than the surface appearance of the somatoplasm. It aims to get at the source or origin of organisms, that is, the *germplasm* which is the only connecting thread between succeeding generations of living forms from the "unbeginning past." It is concerned not so much with somatoplasm, which represents what the germplasm has done in the past, as with the germplasm itself and what it can do in the future.

CHAPTER II

VARIATION

1. The Most Invariable Thing in Nature

In the introductory chapter it was shown that "organic resemblance based on descent," by which is meant heredity, is due principally to the fact that offspring are material continuations of their parents and consequently may be expected to be like them. The fact that this is the case in the great majority of instances has given rise to the popular formula, "like produces like," as a rule of heredity.

But this formula by no means always fits the facts. Like often produces something apparently unlike. For instance, two brown-eyed parents may produce a blue-eyed child, although brown-eyed children are more usual from such a parentage. It is a common experience, indeed, for breeders of plants and animals to meet with continual difficulties in getting organisms to "breed true."

On the other hand, it is exactly these variations which so constantly interfere with breeding true that furnish the sole foothold for improvement. If all organisms did breed strictly true, one generation could not stand on the shoulders of the preceding generation, and there would be no evolutionary advance.

The most invariable thing in nature is variation. This fact is at once the hope and the despair of the breeder who seeks to hold fast to whatever he has found that is good and at the same time tries to find something better. Variation is a veritable Pandora's box and the chaos that would ensue if it were not confined within certain predictable limits can hardly be imagined. Obviously the entire subject of variation is intimately and inevitably bound up with any consideration of genetics, for when the similarities and dissimilarities between succeeding generations are clear, then heredity can be explained.

2. The Universality of Variation

Much of the variation in nature is patent to the most casual observer, but it requires a trained eye to see the universal extent of many minor differences. A flock of sheep may all look alike to a passing stranger, but not to the man who tends them. A dozen blue violet plants from different localities might easily be identified by the amateur botanist as belonging to the same species when, to a specialist on the genus Viola, unmistakable differences would doubtless be clearly apparent.

"Identical twins," for example, constitute so marked an exception to the universal rule of variational difference that they challenge the attention at once, yet even here upon critical examination there appears some degree of variation.

The fact that every attempt at an intimate acquaintance with any group of organisms whatsoever invariably

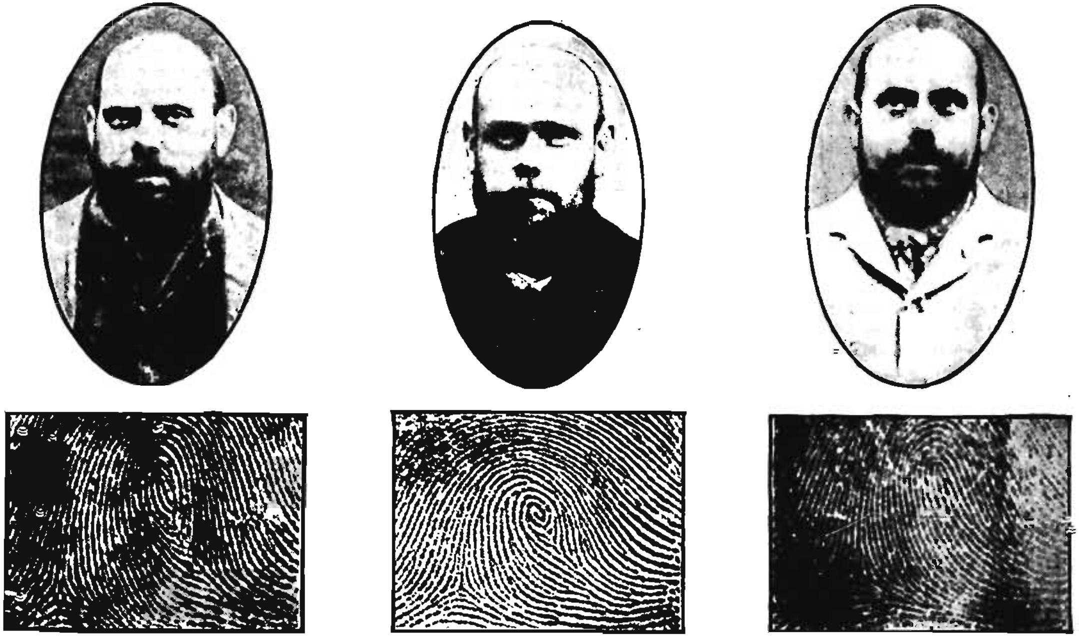


Fig. 4.—The constancy of minor variations. The thumb prints of these three criminals are characteristically different although their faces would easily confuse the ordinary observer. From The Outlook of Feb. 24, 1912.

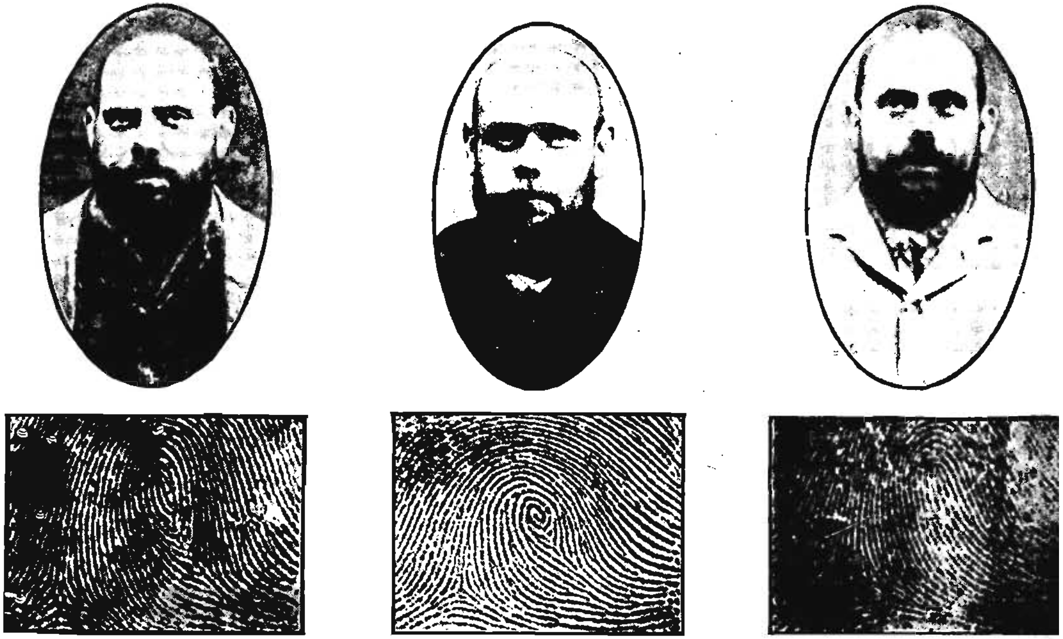


Fig. 4.—The constancy of minor variations. The thumb prints of these three criminals are characteristically different although their faces would easily confuse the ordinary observer. From The Outlook of Feb. 24, 1912.

reveals previously unrecognized variations, indicates that variability is much more widespread in nature than is commonly believed.

The key to Japanese art, as pointed out by Dr. Nitobe, consists in being natural and in faithfully copying nature. It is for this reason that the Japanese artist makes each object that he produces unique, because nature herself, whom he strives to follow, never duplicates anything.

The Bertillon system of personal identification is based upon the constancy of minor variations found in each individual. Its importance is shown in Figure 4. The faces of the criminals there pictured would be easily confused by the ordinary observer, but an examination of their thumb prints shows unmistakable differences between these three individuals.

On the other hand over-emphasis upon the study and analysis of variation may tend to obscure the important fact that parent and offspring in the vast majority of their characteristics are alike.

3. Kinds of Variation

A brief enumeration of some of the kinds of variation will reveal their diverse character.

a. With respect to their nature variations may be morphological, physiological, or psychological. Under *morphological* variations are included differences in shape, size, or pattern as well as differences in number and relation of constituent parts.

Differences in activity are of a *physiological* nature.

The kea parrot, after the introduction of sheep into New Zealand, changed from herbivorous to carnivorous habits and consequently became a pest. Many animals in captivity are less fertile than when free, while different individuals are well known to vary widely with respect to their susceptibility to disease. Nägeli, for example, reports the presence of tubercles in 97 per cent of the cases in five hundred autopsies, although a majority of the deaths in question was not due to tuberculosis at all, a fact which indicates a great diversity in the resistance of different individuals to the tubercle bacillus.

Psychological variations in man, such as those which determine the disposition or mental traits of individuals, are apparent to every one.

b. *With respect to their duplication* variations may be single or multiple. A legless lamb[1] is an example of a *single* variation or "sport." Four-leaved clovers, on the contrary, are *multiple* for the reason that this variation, although not common, nevertheless occurs frequently.

c. *With respect to their utility* variations may be useful, indifferent, or harmful to the organism possessing them. *Useful* variations are of the kind emphasized by Darwin as being effectively made use of in natural selection. *Indifferent* variations, on the other hand, are those which apparently do not play an important part in the welfare of their possessor, such, for example, as the color of the eyes or of the hair. Finally, the degree of degeneration in certain organs may be

[1] "A Peculiar Legless Lamb." Stockard, Biol. Bull. xiii, p. 288.

cited as an illustration of *harmful* variations. The amount of closure of the opening from the intestine into the vermiform appendix in man is an example of a harmful variation, since the larger the opening, the greater is the liability to appendicitis.

d. With respect to their direction in evolution variations may be either *definite* (orthogenetic) or *indefinite* (fortuitous).

Fortuitous or chance variations in all possible directions furnish the repertory of opportunity, according to Darwin, from which natural selection picks out those best adapted to survive in the struggle for existence.

Paleontology furnishes numerous instances of the former category, such as the series of variations from a pentadactyl ancestor, all apparently tending in one direction, which have culminated in the one-toed horse. The fact that the paleontologist deals historically with a completed phylogenetic series in which the side lines lack prominence, while the successful line stands out with distinctness, makes it easy for him to view successive variations as orthogenetic, that is, as definitely directed in one course either through intrinsic (Nägeli) or extrinsic (Eimer) causes.

Just as sometimes the individuals of an apparently continuous series, as shown in a museum collection of similar insects, may be of very diverse geographical origin, so genetics is not primarily concerned with resemblances from generation to generation but rather with origins and continuity.

e. With respect to their source, variations may be somatic or germinal. *Somatic,* or body variations,

arise as modifications due to environmental factors. They are individual differences which may be quite transitory in nature, while *germinal* variations may arise without regard to the environment, are deep-seated, and of racial rather than of individual significance.

f. With respect to their normality variations may fall within expected extremes and thus be considered *normal,* or they may be outside of reasonable expectations and consequently be reckoned as *abnormal,* as in the case of a two-headed calf.

g. With respect to the degree of their continuity variations may form a continuous series, grading into each other by intermediate steps, or they may be discontinuous in character. An example of *continuous* variation is the height of any hundred men one might chance to meet, which would probably represent all intermediate grades from the highest among the hundred to the lowest.

On the other hand the number of segments in the abdomen of a shrimp, for instance, which may be either eight or nine but cannot be halfway between, illustrates what is meant by *discontinuous* variation. The widespread occurrence of this later category of variations has been pointed out by Bateson in his encyclopedic volume "On Materials for the Study of Variation."

h. With respect to their character variations may be quantitative or qualitative. A six-rayed starfish represents a *quantitative* variation from the normal number of five rays, whereas a red variety of a flower may differ chemically from a blue variety, or a bitter fruit

may differ from a sweet fruit in a *qualitative* way dependent upon the chemical constitution of the fruit in question.

i. With respect to their relation to an average standard variations may have a *fluctuating* distribution around an arithmetical mean, as when some of the offspring have more and some less of the parental character, or the variations in the progeny may all center about a new average quite distinct from the parental standard and consequently come under the head of *mutations.*

j. Finally, and most important in the present connection, *with respect to heritability*, variations may possess the power to reappear in subsequent generations, or they may lack that power. It is this aspect of variability which bears most directly upon genetics.

Other possible categories might be mentioned, but a sufficient number have been cited to show the great diversity of variations in general.

4. Methods of Studying Variations

Roughly stated, there are three ways of studying variations: *first,* Darwin's method of observation and the description of more or less isolated cases; *second,* Galton's biometric method of statistical inquiry; and *third,* Mendel's experimental method. The second of these methods will be considered in this chapter.

5. Biometry

The science of biometry, that is, the application of statistical methods to biological facts, has been de-

veloped within recent years. Sir Francis Galton, Darwin's distinguished cousin, may be regarded as the pioneer in this field of research, while Karl Pearson and his disciples are representatives of the modern school of biometricians.

Although mathematical analysis of biological data when not sufficiently ballasted by biological analysis of the same facts may sometimes lead the investigator astray, yet often the only way to formulate certain truths or to analyze data of some kinds is by resort to statistical methods. Biometricians are quite right in insisting that it is frequently necessary to go further than the *fact* of variation, which may be apparent from the inspection of an individual case, and to deal with cumulative evidence as presented through statistical analysis.

In matters of heredity, however, facts as they occur in single cases and definite pedigrees seem to offer a more hopeful line of approach than statistical generalizations. It is better to become acquainted with the real parent than to evolve a hypothetical "mid-parent" mathematically. In this connection it is well always to bear in mind the warning of Johannsen, himself a past master in biometry, when he writes: "*Mit* Mathematik nicht *als* Mathematik treiben wir unsere Studien."

6. Fluctuating Variation

With respect to any measurable character there are bound to be deviations from an average condition. According to the mathematical laws of chance these de-

viations sometimes are plus and sometimes minus, and consequently they may be termed *fluctuating variations.*

Pearson gives as a simple illustration of fluctuating variation the number of ribs present in two sets of beech-leaves, as shown below. These sets were taken from two different trees, and each contains twenty-six leaves.

Number of Ribs	13	14	15	16	17	18	19	20	Total
First tree			1	4	7	9	4	1	26
Second tree	3	4	9	8	2				26
Total	3	4	10	12	9	9	4	1	

It will be seen that, while certain leaves might well belong to either tree, as, for example, those with sixteen ribs, the entire group of leaves from either tree is unlike that of the other tree. In the first instance the number of ribs fluctuates around eighteen as the commonest kind; in the second case, around fifteen. Such a difference could not easily be detected or expressed by any other method than the statistical one.

Again, in the case of forty-seven starfishes all of which were collected from one locality the variation in the number of rays proved to be, according to Goldschmidt, an amount indicated graphically in Figure 5, where the data are arranged in the form of of a so-called frequency polygon or curve.

From such a polygon certain *constants* may be computed which conveniently express in a single number, for purposes of abstract comparison, distinctions that

otherwise could be handled only in the most indefinite way.

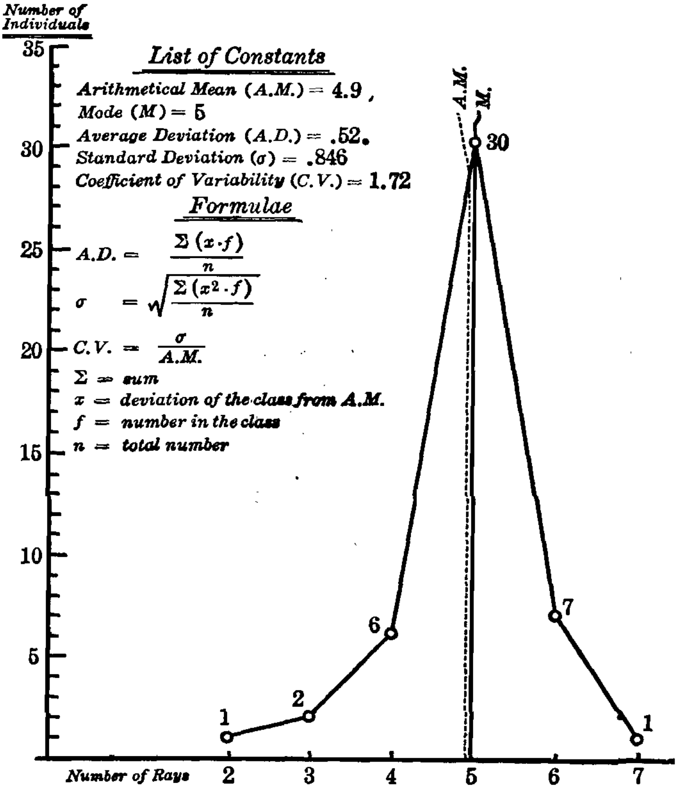


Fig. 5.—The fluctuating variability of starfish rays. From data by Goldschmidt.

Thus in this instance the *arithmetical mean*, expressed by the hypothetical number 4.915, a number which of course does not actually occur in nature, is

simply the average number of rays in forty-seven starfishes selected at random.

The *mode* which represents the group containing the largest number of individuals of a kind, namely, thirty out of forty-seven, is five in this particular polygon. If all individuals fell within the mode there would be no variation and the polygon would become a vertical line.

The *average deviation,* which is an index of the amount of variation going on among the starfishes in question, is .52. In other words, .52 is the average amount that each individual starfish deviates from the arithmetical mean of 4.915. Although the one seven-rayed starfish which happens to be in the lot varies from the standard of 4.915 to the extent of 2.085 (7—4.915) rays, there are thirty five-rayed starfishes which vary only .085 (5—4.915) of a ray, and consequently the average of the entire forty-seven amounts to .52 of a ray. In another collection of starfishes where either more seven-rayed or two-rayed specimens might be present, the average deviation would probably be greater.

By computing the average deviation, therefore, and using it as the criterion of variation, a comparison of the variability of organisms that have been taken from different localities or subjected to different conditions can be definitely expressed.

A measure of variability more commonly in use by biometricians, because of its relation to probable error, is the *standard deviation.* This is the square root of the sum of all the deviations squared and their

frequencies divided by n, according to the formula

$$\sigma = \sqrt{\frac{\Sigma\,(x^2 \cdot f)}{n}},$$

in which x represents the deviation of each class from the arithmetical mean; f, the number of individuals in each separate class; Σ, the sum of the classes; and n, the total number of individuals.[1]

In the present instance the standard deviation is .846, a number that has valuable significance only when brought into comparison with standard deviations similarly derived from other groups of starfishes.

Such a variation polygon as the above expresses the law that the farther any single group is from the mean of all the groups making up the polygon, the fewer will be the individuals representing it.

7. The Interpretation of Variation Curves

a. Relative Variability

The statistical determination of the relative variability of two lots of organisms with respect to a certain character may be illustrated by the case of the oyster-borer snail, *Urosalpinx cinereus*, as seen in the accompanying table on page 29.

The obvious conclusion to be drawn from this table is that the snails which were unintentionally carried from the Atlantic coast to California in the transplantation of oysters show more variation in their new habitat than they did in the old one with respect to the

[1] For directions explaining the use of such formulæ see Davenport's "Statistical Methods."

ATLANTIC AND PACIFIC SHELLS COMPARED

Locality		Number of Shells	A.M.	σ	Probable Error
Woods Hole	West Shore	1,001	58.928	2.339	±.0352
	Penzance Point	1,002	61.718	2.737	±.0412
	Nobska Point	1,002	61.737	2.152	±.0324
	Nobska Point	1,001	61.944	2.234	±.0337
	Nobska Point	496	66.944	2.366	±.0507
	Barnacle Beach	998	63.932	2.604	±.0393
	Big Wepecket	1,006	57.426	2.052	±.0308
	Mid-Wepecket	500	57.606	2.098	±.0447
	Average for Mass.		61.066	2.335	±.0386
California	Belmont Beds	1,008	59.051	3.023	±.0454
	San Francisco Bay	520	60.892	3.361	±.0703
	Average for Cal.		59.664	3.138	±.0538
	Difference			.803	

particular character measured, namely, the relative size of the mouth aperture compared with the height of the entire shell.[1]

A further analysis of the data in this particular case shows that this conclusion is probably biologically incorrect, a discovery which does not invalidate it, however, as an illustration of a method of determining relative variability.

b. *Bimodal Polygons*

Sometimes two conspicuous modes make their appearance in a frequency polygon, as Jennings found, for example, in measuring the body width of a population of the protozoan *Paramecium* (Fig. 6).

[1] "Variation in Urosalpinx." Walter. Amer. Nat. 1910, Vol.

It was subsequently found that the two modes in this polygon were due to the fact that the material in question was a mixture of two closely related species, *Paramecium aurelia* and *Paramecium caudatum*, the

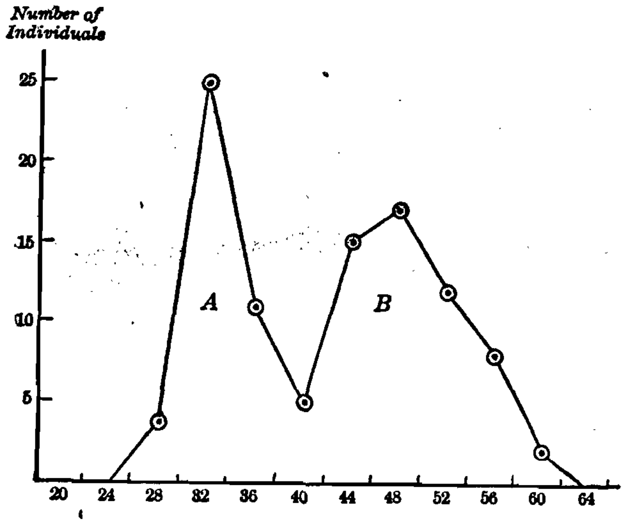


FIG. 6.—The body width of a population of the protozoan *Paramecium*, showing a polygon with two modes. *A*, *Paramecium aurelia*. *B*, *Paramecium caudatum*. After Jennings.

individuals of which arranged themselves around their own mean in each instance.

Although such an explanation does not always turn out to be the right one, the biometrician is led to suspect when a two or more moded polygon appears that he is dealing with a mixture of more than one kind of material, each of which fluctuates around its own average. Heterogeneous material, it should be noted, does

not always give a bimodal curve. For example, if Pearson's two lots of beech leaves mentioned above are mixed together, they form a regular series from the inspection of which no one could infer their double origin. (See the heavy line in Figure 7.)

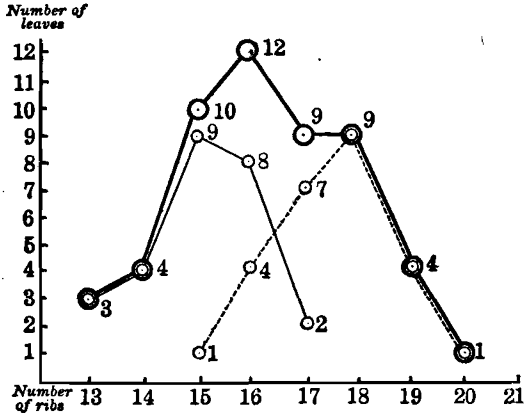


FIG. 7.—The ribs of leaves from two beech trees. When put together they form a polygon which does not reveal its double origin. From data by Pearson.

c. Skew Curves

The direction in which variations are tending may sometimes be determined by the statistical method. As an illustration of this may be cited the number of ray florets in 1000 white daisies (*Chrysanthemum leucanthemum*), 500 of which were collected at random by the writer from a small patch in a swampy meadow in northern Vermont, while the other 500 were selected in the same random manner upon the same day from a dry hillside pasture hardly more than a stone's throw

distant. Among these two lots of daisies the number of ray florets varies from twelve to thirty-eight and their frequency polygons, as shown in Figure 8, form what are termed "skew curves," because the mode in

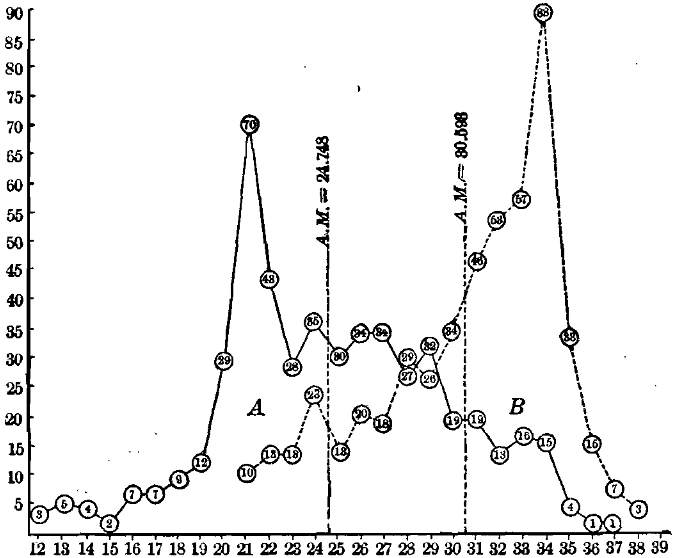


FIG. 8.—Variation in the ray florets of the white daisy (*Chrysanthemum leucanthemum*). *A*, from a swampy meadow. *B*, from a dry hillside pasture near by. Both the curves are "skew" because in each case there is an admixture of the other type. The distinction between the two types is due to heredity rather than to environment.

each case lies considerably to one side of the arithmetical mean.

It will be seen that lot *A* from the swampy meadow, which in spite of the greater fertility of the soil and the unquestionably greater luxuriance of the plants themselves, produced heads with fewer florets, fluctu-

ates around the number 21, while the dry pasture population *B*, characterized by blossoms which were in general noticeably smaller, fluctuates around the number 34. The habitats of the two lots were so near together, however, that there was probably a considerable intermixture of the two types, as shown by the tendency of each polygon to produce a second mode. Thus the *A* polygon shows that there is an increasing tendency or variability in the twenty-one floret type toward the thirty-four floret type, due probably in this particular instance to invasion resulting from the proximity of the *B* colony.

8. Graduated and Integral Variations

It is comparatively simple to treat statistically *integral* variations, illustrations of which have been given in the case of beech-leaf ribs, starfish rays, and daisy florets, all of which are characters that can be readily counted. In the same way any measurable character, such as the size of snail shells, may fall into easily limited groups, as, for example, 10 to 11 mm., 11 to 12 mm., 12 to 13 mm., etc. It is somewhat more difficult to classify variations when color or pattern is the character in question, since it then becomes necessary to define certain arbitrary limits for each class of the series within which to group the individual variants.

Tower, in his famous researches on potato-beetles, encountered variations in the pigmentation of the pronotum all the way from entire absence of color to com-

plete pigmentation but by cutting up this continuous series of variations into arbitrary groups of equal extent, it was quite possible to arrange the data so that they could be statistically treated just as conveniently as the integral variations mentioned above. Groups or classes of this kind are termed *graduated* variations.

9. The Causes of Variation

With respect to the causes of variation authoritative biologists have taken different points of view.

a. Darwin considered variations as axiomatic. An axiom is self-evident, requiring no explanation. The absence of variations in organisms rather than the occurrence of variations is, from this point of view, the phenomenon requiring an explanation. Although Darwin himself spent some time in pointing out the universal occurrence of variability, he accepted it as a primary fact and proceeded from it as a starting point without attempting to seek its causes.

b. Lamarck and his followers have regarded the causes of variation either as extrinsic, that is, referable to external factors making up the environment of the organism, or as intrinsic or physiological, that is, based upon the efforts which an organism puts forth to fit into its particular environment successfully. The causes of variation are to be sought according to the Lamarckian school, in the "environment" and "response" sides of the triangle of life rather than in the "heritage" side (Fig. 1).

For example, Woltereck, by controlling the single

extrinsic factor of food supply, was able to modify the height of the "head" of the microscopic fresh-water crustacean, *Hyalodaphnia*, in the remarkable manner indicated in Figure 9. When poor food was supplied, the percentage of the head height to that of the body averaged hardly forty, while with rich food it was increased to over ninety.

Similarly Klebs succeeded in changing at will the

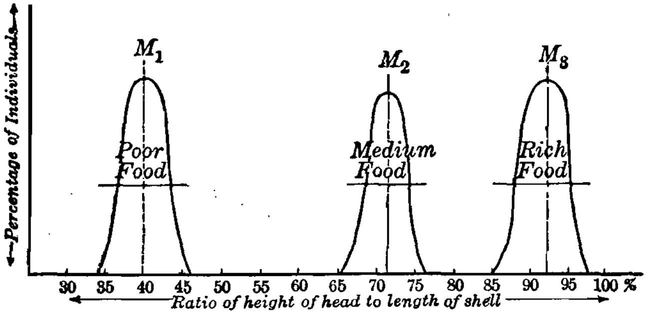


Fig. 9.—Schematic curve of the head height of *Hyalodaphnia* under various conditions of nourishment. Adapted from Woltereck.

number of stamens in the common "live-for-ever," *Sedum spectabile*, by manipulating the environment in which the plants were kept. Some of his results are shown in Figure 10. Curve *A* combines the data for 4260 flowers which were raised in well-fertilized dry soil under bright light; curve *B* represents 4000 flowers grown in a moist greenhouse under red light; and curve *C* includes 4390 flowers from well-fertilized soil in moist hotbed conditions under a weak light.

c. Weismann, on the contrary, believes that the

causes of variation, at least of heritable variations are intrinsic or inborn in the germplasm. His conception of sexual reproduction is that it is a device for doubling the possible variations in the offspring by the mingling of two strains of germplasm (*amphimixis*). By far the greater number of observations recorded go to substantiate this theory.

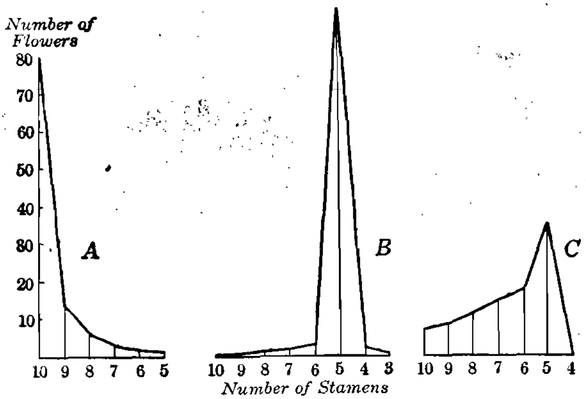


FIG. 10.—Variations in the number of stamens in the flowers of the "live-for-ever" (*Sedum spectabile*) under various controlled conditions. For detailed description, see text. After Klebs.

Tower found among his potato-beetles, for example, that two strains reared in the same environment showed striking differences in variation, a fact necessarily due to intrinsic rather than to extrinsic factors. Similar cases may be recalled by any one.

Nevertheless, heritable variation occurs in the absence of amphimixis so that, at best, sexual reproduction furnishes only one of the possible avenues for the introduction of hereditary variations.

a. Lastly, *Bateson*, whose work "On Materials for the Study of Variation" already cited is a classic, takes the agnostic attitude that it is rather futile to guess at the causes of variation before the facts are well in hand. He consequently discourages such attempts by saying: "Inquiry into the causes of variation is, in my judgment, premature."

In conclusion, the words of Darwin written over half a century ago: "Our ignorance of the laws of variation is profound," may still be appropriately quoted, notwithstanding the fact that in biometry we have at least an excellent analytical method by means of which considerable insight into variation is being gained.

CHAPTER III

HERITABLE DIFFERENCES

1. The Mutation Idea

Variety is not only the "spice of life" but it is also the central necessity in the origin of new kinds of animals and plants. If there was no variation from generation to generation then nothing new would appear which nature could in any way seize upon in order to escape from conservative monotony and as a result there would be no possible evolution in any direction. This deplorable state of affairs we know is contrary to fact.

There are at least three ways, according to Baur, by which an organism can become different from its relatives, viz.—1, modification; 2, combination; 3, mutation. Which of these three ways has been followed in any specific instance can only be determined with certainty by the test of subsequent breeding, for there is nothing in the appearance of an animal or plant to indicate by which of these three paths it has gained any distinctive variation.

By *modifications* we understand those widespread differences which are the result of nurture rather than nature. They are simply environmental effects upon the somatoplasm and consequently are, in all probabil-

ity, transitory so far as their inheritance is concerned. They are the result of soil rather than seed.

"Combinations" and "mutations" are more deep-seated. They are conditioned by the germinal nature of the organism and may, therefore, be passed on as hereditary.

Combinations are the result of a new deal after a reshuffling of the cards. Nothing essentially new, which was not already present in one or the other of the parental lines, is introduced but a different arrangement or bringing together of old qualities is effected. This process of variation through hybridization is the concern of Mendelism and will be considered further on.

Mutations, like Minerva springing full-fledged from the head of Jove, are something *qualitatively* new which appear abruptly without transitional steps and that breed true from the very first.

A distinctive qualitative character marks mutations, like the discontinuous differences between such chemical compounds as carbon monoxide (CO) and carbon dioxide (CO_2), as Bateson has pointed out, but the leap from one to the other may be so small that it is difficult to ascertain by inspection whether the difference is due to mutation or to modification. *The test comes in breeding*, since the progeny of a modification, or "fluctuation" as deVries terms it, will revert to the old average of the parental generation, while the progeny of a mutation will vary around a new average set by the mutation itself.

The series of positions taken by the lower end of a swinging pendulum illustrate what is meant by these

non-heritable fluctuating modifications. They all hold predictable relations to the average position shown when the pendulum comes to rest, because whenever the pendulum is put in motion the various positions all recur as before. A mutation, on the contrary, is represented by a change in the point of attachment at the upper end of the pendulum. It occurs only when the entire pendulum is unhooked and hung up in a different place. This new point of attachment must be chosen arbitrarily and has no such definite relation to the original attachment as characterizes the variation in position of the swinging end of the pendulum.

When the attempt is made to arrange a series of successive mutations in a curve they do not show a graded relationship to each other as fluctuations do. The latter mass around the average standard according to the laws of chance in much the same way that a hundred shots by a good marksman may center around a bull's-eye. Mutations never group in this way. They find no correspondence even with wild shots at the bull's-eye. They are shots directed at a different target altogether. To use the musician's phraseology, a variation elaborated upon an old theme would correspond to a *modification* but a *mutation* would be an entirely new theme.

Darwin was fully aware of the existence of mutations or "sports" as he called them, and incidentally gave time to their consideration, but the great task which he set out to accomplish in such a masterly manner was to overthrow the widespread and deep-seated belief of his day in a sudden special creation of distinct

species. To this end he marshaled evidence in support of the gradual transition of one species into another, emphasizing fluctuating modifications rather than mutations which seemed to him to play a minor rôle in the origin of species.

It remained for the Dutch botanist Hugo deVries to be the first to analyze the character of mutations and to focus attention upon them. There is something distinctly suggestive of Darwin's method in the fact that deVries worked in silence for twenty years before he gave the world the "Mutationstheorie" with which his name will be forever connected.

2. A Summary of the Mutation Theory

The main features of the mutation theory of deVries may be indicated as follows:—

a. New species arise abruptly regardless of environment without transitional forms, and at present they are not known to arise in any other way.

b. New forms arise as unusual deviations from the parent form, which itself remains unchanged although it may repeatedly give rise to similar deviations.

c. New mutations are, from the first, constant, that is, they produce their like. They do not become gradually evolved, as the result of natural selection although natural selection may act upon them after they appear.

d. Among mutations there may occur forms characterized by the addition of something new,—*progressive elementary species*,—as well as forms lacking

something present in the parental type,—*regressive varieties.*

e. The same mutation may arise simultaneously in many individuals instead of as a single "sport."

f. Mutations do not vary around an arithmetical mean with respect to the parent form, as is the case with fluctuating variations, but each fluctuates around a new average of its own, thus forming a discontinuous series with the parent form.

g. Mutations may occur in all directions, that is, they are not necessarily definite or orthogenetic.

h. Mutations probably appear periodically.

i. Every mutation means two possible species where one existed before.

j. Useless or insignificant fluctuating variations are not necessarily the material from which natural selection must sift out new species.

k. Natural selection is not a causative agent in evolutionary advance but is simply a sieve which picks out successful survivors from mutations.

3. Lamarck's Evening Primrose

Perhaps the most widely known plant mutations are the progeny of Lamarck's evening primrose, *Œnothera lamarckiana*, because it was these plants that led deVries to formulate his mutation theory.

It is believed by botanists in general that this plant is a native of the southern United States, although, so far as is known, it is now extinct as a wild species in America, and native specimens are included in but few American herbaria.

It was exported to London as a garden plant about

1860, and thence it spread to the continent, where, escaping from gardens, it became wild in at least one locality near Hilversum, a few miles from Amsterdam. Here, in an abandoned potato field, it fell under the seeing eye of Hugo deVries in 1885, and now both botanist and primrose are famous.

DeVries found among these escaped plants not only *O. lamarckiana*, but also two other kinds of mutants, *O. brevistylis*, characterized by short-styled flowers, and *O. lævifolia*, which has smooth leaves. These two were entirely new species hitherto unknown at the great botanical clearing-houses of Paris, Leyden, and the Kew Gardens.

Since the seeds of the *Œnothera* are produced by self-fertilized flowers, deVries felt safe in regarding these plants as mutants rather than hybrids, and he continued to study them with especial care. Transplanting the mutants along with representatives of *O. lamarckiana* to his private gardens in Amsterdam, where it was possible to maintain them in normal healthy condition, deVries was able to follow their individual histories with certainty.

The wild mutants *lævifolia* and *brevistylis* did not reappear under cultivation but he found that, out of 54,343 plants of the species *O. lamarckiana* grown as descendants from nine original plants during eight years, there appeared 837 mutants comprising seven different elementary species, all of which, with the exception of *O. scintillans*, bred true. See table on the next page.

Some explanatory comment on this table may be of value.

Mutants of Œnothera lamarckiana

Generation		Gigas	Albida	Oblonga	Rubrinervis	Lamarckiana	Nanella	Lata	Scintillans	Total
I	1886–7					9				
II	1888–9					15,000	5	5		
III	1890–1				1	10,000	3	3		
IV	1895	1	15	176	8	14,000	60	73	1	
V	1896		25	135	20	8,000	49	142	6	
VI	1897		11	29	3	1,800	9	5	1	
VII	1898			9		3,000	11			
VIII	1899		5	1		1,700	21	1		
		1	56	350	32	53,509	158	229	8	54,343

The seeds in each generation were self-fertilized *lamarckiana.*

The mutant *gigas* occurred once, in 1895. From the seeds of this one plant were produced 450 true *gigas* offspring in the first year, and the strain continues to breed true.

Albida was first noted in 1895, but deVries remembered having seen it before and dismissing it as pathological. Because of its poverty in chlorophyll it is a mutant which probably would not maintain itself successfully in nature, but it breeds constant under cultivation.

Oblonga always bred true with the exception of throwing an *albida* in 1895 and a single example of *rubrinervis* in 1899.

Of *rubrinervis* over 2000 invariably bred true, while *nanella* bred true in over 20,000 offspring, with but three exceptions when *oblonga* characters appeared.

Lata, since it produces only female flowers and so cannot be self-fertilized, had constantly to be crossed back with the parent *lamarckiana*, when it produced from 15 to 20 per cent *lata* and 80 to 85 per cent *lamarckiana.*

Finally, *scintillans* which appeared at three separate times proved constant only in its inconstancy because it invariably produces a heterogeneous progeny. The 1895 plant gave 53 per cent *lamarckiana*, 35 per cent *scintillans*, 10 per cent *oblonga*, and 1 per cent *lata*. One of the 1896 plants gave 51 per cent *lamarckiana*, 39 per cent *scintillans*, 8 per cent *oblonga*, 1 per cent *lata*, and 1 per cent *nanella*, while another 1896 plant gave only 8 per cent *lamarckiana*, but 69 per cent *scintillans*, 21 per cent *oblonga*, and 2 per cent of *nanella* and *lata* together.

These different kinds of evening primroses are distinguished from each other by features which are unmistakable even to the uninitiated. The old-time systematist would undoubtedly have regarded them as distinct species.

DeVries distinguishes four categories among the *Œnothera* mutants, the first three of which are quite likely to maintain themselves in nature. They are:—

1. *Progressive species*, (*gigas*, *rubrinervis*), due to the addition of certain characteristics;
2. *Retrogressive varieties*, (*nanella*, *læviflora*, *brevistylis*), characterized by the loss of something that was present in the parent form;

3. *Inconstant species*, (*scintillans* and *lamarckiana* itself), that do not always breed true but produce mutants, and
4. *Degressive species*, (*lata*, *albida*), which are defective in some way and are incapable of maintaining themselves in nature.

DeVries' experiments and observations have been repeated on a large scale and extended, notably by MacDougal in the New York Botanical Gardens, by Shull at the Carnegie Institution for Experimental Evolution, Cold Spring Harbor, Long Island, and by Gates in England, and his conclusions have been confirmed in all essential points. The mutability of *O. lamarckiana* is as unmistakable and as diverse in America and England as it is in Holland.

The critics of deVries, however, regard *Œnothera lamarckiana* as a hybrid to begin with, from which different strains have simply been bred out. Both Bateson and Lotsy have called attention to the presence of deformed or defective germ cells in *Œnothera lamarckiana* as evidence of its hybridity, and Davis, by crossing *O. franciscana* and *O. biennis*, has produced a hybrid *Œnothera*, which he has christened *Œnothera neo-lamarckiana* because it not only resembles *O. lamarckiana* but behaves like it in producing mutations. He consequently proposes "dissolution of hybrids" as a substitution for mutation in explaining the phenomena that deVries has described.

It is somewhat questionable whether this classical plant, which has added at least a five-foot shelf to

the biological literature of the last thirty-five years, is after all the most fortunate organism for demonstrating mutation since its "mutations" may represent simply combinations becoming isolated from something already present as the result of past hybridization. In either case the new form would breed true and behave like a true mutation.

4. Plant Mutations found in Nature

The oldest known authenticated case of a plant mutation is the oft cited instance of the "fringed celandine," *Chelidonium laciniatum*, which made its appearance in the garden of the Heidelberg apothecary Sprenger in 1590 among plants of the "greater celandine," *Chelidonium majus*. The fringed celandine bred true at once and is now a widespread and well-known species.

The purple beech has appeared historically as a mutant among ordinary beeches upon at least three occasions in widely separated localities, and it has always given rise to a constant progeny.

The "Shirley poppy," notable for its remarkable range of color, which was discovered in 1882 by Rev. W. Wilks, originated from a single plant of the small red poppy, *Papaver rhœas*, which is commonly found in English cornfields.

The first double petunia was found in 1855 in a private garden in Lyons. (Ziegler.) Other instances are known of double flowers among roses, azaleas, stocks, carnations, primroses, etc., arising from single

flowering plants, the seeds of which in turn produce double flowers.

The giant primrose is a mutation from a normal strain of known pedigree. (Keeble.)

"Mutations in certain pericarp color patterns of maize are so common that a wide range of variability results. Selection is able from such material to isolate types relatively stable but very diverse in appearance." (Emerson and Hayes.)

That plant mutations may occur in nature and persist successfully without isolation or external selection is shown, for instance, by Schaffner [1] who reports an unusual white verbena growing wild in Ohio over about a square mile of territory along with the typical purplish blue *Verbena stricta* without transitional forms.

Hayes discovered a tobacco mutant in which the average number of leaves produced was 70 instead of 20, and Cockerell found a single red mutant plant of the sunflower, *Helianthus lenticularis coronatus*, which has bred true. The list of similar plant mutations could be almost indefinitely extended.

5. Some Mutations among Animals

In 1791 a Massachusetts farmer, by name Seth Wright, found in his flock of sheep a male lamb with long, sagging back and short, bent legs resembling somewhat a German dachshund. With unusual foresight he carefully brought up this strange lamb because it was an animal that could not jump fences

[1] Ohio Naturalist. Dec., 1906.

It occurred to this hard-headed Yankee that it would be much easier to get together a flock of short, bow-legged sheep, unable to negotiate anything but a low hurdle, than to labor hard at building high fences. So it came about that this mutating lamb, in the hands of a man who appreciated labor-saving devices, became the ancestor of the Ancon breed of sheep. Later on this breed gave place in public favor to another mutant, the Merino, which produces a superior grade of wool.

Some mutations, however, that may be selected and maintained by man are unlikely to succeed in nature when left to themselves. Albino animals, for example, are so handicapped by defective eye-sight that they have a hard struggle in the wild condition. Albino rats set free by Dr. Hatai a few years ago upon Goose Island, a small uninhabited bit of land in Long Island Sound, all succumbed to the native rats in a short time.

Hornless cattle suffer fewer injuries from one another than horned cattle. It has consequently become quite a general practice among farmers to "dehorn" their stock surgically. It is an obvious advantage to have cattle born hornless, and many breeds having this character are now established. In 1889 a mutant among horned stock appeared at Atchison, Kansas, in the form of a hornless Hereford. From this mutant has descended the well-established race of polled Hereford cattle, constituting a bovine aristocracy with registry books and blue blood all their own.

Taillessness in cats, dogs and poultry, as well as

ther instances of mutations.

Davenport,[1] writing of his experiments with poultry, says: "During the past four years I have handled and described over 10,000 poultry of known ancestry. Of striking new characters I have observed many, some incompatible with normal existence; others in no way unfitting the individual for continued life. In the egg unhatched I have obtained Siamese twins, pug jaws, and chicks with thigh bones absent. There have been reared chicks with toes grown together by a web, without toenails or with two toenails to a toe; with five, six, seven, or three toes; with one wing or both lacking; with two pairs of spurs; without oil-gland or tail; with neck devoid of feathers; with cerebral hernia and a great crest; with feather shaft recurved, with barbs twisted and dichotomously branched or lacking altogether. Of comb alone I have a score of forms. All of these characters have been offered to me without the least effort or conscious selection on my part, and each appeared in the first generation as well-developed peculiarities, and in so far as their inheritance was witnessed, each refused to blend when mated with a dissimilar form."

Bateson (1894), in his "Materials for the Study of Variation," gives a detailed list of 886 cases of "discontinuous variations" among animals, many of which doubtless belong to the category of mutations, al-

[1] Davenport, C. B., 1909. "Inheritance of Characteristics in Domestic Fowl." Carnegie Institution of Washington, Publication No. 121.

placed even in the non-inheritable class of "freaks."

The chief reason why definite examples of mutation are so infrequently noted and recorded is because the attention of the investigator has generally been directed, not to them, but to gradual fluctuating variations which, according to Darwin's conception, furnish the material for the operation of natural selection. Mutations are doubtless much more common than has been generally supposed, and it is likely that they will receive more attention in the future than they have in the past.

No stock when bred on a large scale breeds absolutely true for all specific characters. Gerould reports that in his butterflies (*Colias*), he found blue-green instead of yellow-green eyes, uncoiled instead of coiled tongue, the absence of orthodox wing spots, one proleg less in the caterpillar, etc. *Drosophila* is a famous example of many deviations from type which have been revealed upon persistent and careful scrutiny.

6. Kinds of Mutation

Multiple or *aggregate mutations* are those germinal upsets that affect many parts of an organism instead of a single part. This type is of frequent occurrence and is in contrast to a *single gene mutation* which involves only an hereditary unit that determines a single somatic feature. For example, Babcock describes a new walnut, *Juglans quercina*, which appeared inde-

pendently in four different widely separated localities in California. This, like deVries' evening primrose, was an aggregate mutation, for differences appeared in size, shape, color and texture of leaves; size, form and color of flower-parts; color of bark, habit of growth, etc. That this was a true mutant and not a hybrid between the oak and the walnut was indicated by negative results in cross-pollinating experiments. Similar aggregate mutations have been reported for cotton, tomato, tobacco and other organisms.

Another phenomenon that probably indicates common ancestral germplasm among species, at present apparently independent of each other, is the occurrence of *parallel mutations.* The North African ostrich (*Struthio camelus*) and the South Australian ostrich (*S. australis*), although separated from each other for long geological time, show, according to Duerden, similar mutations in size, length of neck and legs, skin-color and bald-head as well as in size and shape of the egg and the character of its surface, whether pitted or ivory-smooth.

A long list of parallel mutations in *Drosophila melanogaster* and *D. virilis* has been described by Metz, and similarly, Sturtevant reports mutations in *D. funebris* that are likewise parallel to those of *D. melanogaster,* in which the occurrence of mutations has probably been more carefully studied than in any other animal.

Sumner with the deer-mouse, *Peromyscus,* has found albinism, spotting and red-eyed yellow, all mutations known to occur in other mice.

Reverse mutations have also been repeatedly observed. This is something resembling the unscrambling of an egg. Morgan and Bridges obtained, for example, normal red-eyed flies from white-eyed mutants and May, also with ubiquitous *Drosophila*, got back normal-eyed individuals from bar-eyed mutants.

The frequent occurrence of *recurrent mutations*, that is, the reappearance of the same mutations, suggests that the cause underlying these irregular hereditary changes is something continuous and definite even if we are at present unable always to put our finger upon it. The evening primroses have repeatedly shown the same mutations in widely different localities and under the eyes of different investigators. Morgan says of his famous banana flies, "One of the first mutants that appeared, viz., white eyes, has appeared anew in our cultures about three times, in cultures known to be free from it before and not contaminated. The same mutant has been found by several other observers. The eye color vermilion has appeared at least six times; the wing character called rudimentary, five times; cut wing has been found four times," etc.

7. The Origin of Mutations

Mutations may be *gametic*, *zygotic* or *somatic* in their origin. There seems to be no reason why mutation may not occur at any stage in the life-cycle of an organism. In the first place, it may be *gametic* in origin if the onset is in the germ-cell before or during the maturation changes that prepare it for union with

another germ-cell (See Chap. X). In this instance its effect may be profound and patent upon the entire development of the individual, although if it chances to be relegated to an abortive polar cell during meiosis or to an unmated spermatozoon it will be entirely lost at once. There are no doubt many such "mute inglorious mutations" (Muller) that never see the light of day.

It is furthermore obvious that a gametic mutation usually enters the organism concerned *singly*, that is, from one parent only, and if recessive in character will fail to put its appearance in the somatoplasm until some subsequent generation when two hybrids from the new stock each chance to contribute the recessive mutant character in question to the formation of a new individual.

The appearance of such mutants, therefore, unless dominant, must come two or more generations after the mutation has taken place. The time when a gametic mutation is initiated, consequently, and when it manifests itself are by no means necessarily the same. This fact needs to be kept in mind in considering the evidences from experiments for the determining causes of mutations.

Perhaps the reason why mutations are more frequently reported in self-fertilizing (autogamous) plants than in cross-fertilizing (heterogamous) animals is because in self-fertilizing organisms the inbreeding necessary to bring about the doubling of a single character so that it will come into expression is more likely to occur.

Secondly, the mutation may occur in the fertilized egg. This is *zygotic mutation.* In this case the change is evident at once in the resulting individual since the developing individual is the *unfolding* of what is present in the zygote. Such a mutation, for example, occurring *after fertilization* and not as the result of a combination or cross, is reported in tobacco by Hayes and Beinhart.[1]

Thirdly, in contrast to the two kinds of mutations just described which are distinctly germinal in origin, there may be *somatic mutations* which fall directly upon some individual somatic cell or tissue arising out of the original germplasm and produce in turn such abnormalities as "bud variations," chimæras and the like. In such a case all the cells and tissues arising from the mutant somatic cell will express the mutation and no others. Lehmann, 1920, proposes the term *metaclonosis* for hereditary somatic modifications, reserving the term *mutation* for solely those instances that involve a change in the genes.

8. When Mutations Occur

It has been suggested by Standfuss that species may go through the same kind of a life-cycle that individuals do, only taking infinitely more time to do it. As shown in Figure 11, they are born of other species and enter the prodigious growth period of infancy and youth, both of which are characterized by much fluctuation. With maturity they gradually become comparatively stable until the reproductive period is reached,

[1] Science XXXIX, No. 992, p. 34.

when they throw off their progeny, as on a tangent. They finally pass into the excessively differentiated period of old age, from which there is no recall, although they approach in many features the infantile condition, and end in death or extinction. This cycle is repeatedly illustrated by phylogenetic lines of fossil forms which have long since become extinct.

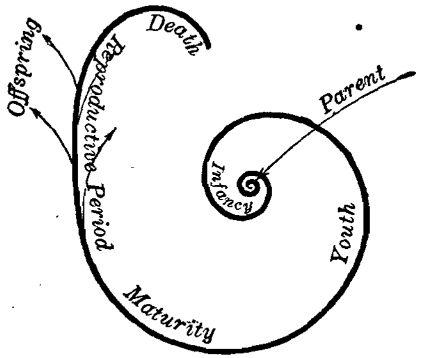


FIG. 11.—Diagram of the relation of reproduction to the life-cycle.

Beecher has pointed out that, in paleontological times just before they became extinct, species often underwent extreme specialization in the form of fantastic shapes, an excessive number of spines or elaborate sculpturings on the shells as seen among the ammonites, belemnites, and trilobites, or of gigantic size as in the dinosaurs, plesiosaurs, and theromorphs. All of these facts indicate a *species-cycle* in which these abnormal features were the unmistakable signs of old age.

The reproductive period of a species when mutants are being thrown off, as of an individual, may extend over a considerable period of the whole cycle, or it may be confined to a relatively small segment. It is possible that in the evening primrose deVries may

have caught a plant passing through the crucial period of species-reproduction.

Another reason why so few mutations have as yet been seen may be because the majority of organisms are not, during the short span of human observation, in the reproductive part of their cycles. When it is remembered that accurate observation with this object in view has extended over only a brief period, insignificant in comparison with the vast geologic stretches of time concerned in species-building, the marvel is that so much, rather than so little, has been seen.

9. Possible Causes of Mutation

There are at least three avenues of approach to the analysis of mutation: (1) *Anatomical*, depending upon observation of its occurrence in nature and under control; (2) *Genetical*, consisting of the experimental breeding of test cases, and (3) *Cytological*, or the microscopic examination of the germplasm. It is this latter method that furnishes perhaps the most hope of gaining some insight into the fundamental causes underlying the phenomena of mutation.

No doubt the conclusions in this paragraph could be better presented after the consideration of the remaining chapters of the book, particularly the section on the cellular basis of heredity (Chaps. X, XI and XIII), but some discussion, nevertheless, seems desirable at this point, even if it may be necessary to return and reread it later.

Babcock and Clausen have classified mutations from

the cytological standpoint into two groups, viz., *chromosomal aberrations* and *factor mutations*. Chromosomal aberrations are accidents or irregularities occurring in the nuclear make-up of the germ-cells. These aberrations may be of various kinds and probably take place during meiosis when the germ-cells are going through the preparatory process of reduction of the chromosomes which precedes the formation of the fertilized egg.

For example in the unpairing of homologous chromosomes after synapsis it is conceivable that the process may not be clean-cut and complete but that a piece of one chromosome may adhere to its mate thus changing its size and composition. Or again, a fragment of a chromosome, during the complicated elimination performances accompanying the marriage ceremony of germ-cells, may be shuffled out and lost, thus creating a deficient chromosome. Such accidents to the germ-cells would be reflected in all the subsequent mitotic divisions of the somatic cells derived therefrom and a mutation would be the result. At any rate an examination of the nuclear structure of mutants frequently reveals chromosomal irregularities so that an unmistakable relation between the two phenomena undoubtedly exists.

Another irregularity that occurs is an unequal migration of the chromosomes to the poles of a germ-cell during the reduction division, which, of course, results in a cell progeny of mature gametes having a number of chromosomes unlike the number in the normal gametes. This appears to be the reason for

the mutation, *Œnothera lata*, which has 15 chromosomes instead of 14, the typical number for *O. lamarckiana* from which it sprang. What occurs in the formation of this mutation is that for some reason *O. lamarckiana* during reduction division instead of dividing as usual into 7-7 makes the unequal division of 6-8, a phenomenon known as *non-disjunction* (Bridges). When this 8-chromosome gamete joins with a normal 7-chromosome gamete the new mutant number of 15, characteristic of *O. lata*, is the result.

Gates and others in their extensive cytological studies on *Œnothera* mutants, have found not only 15 chromosomes instead of 14 but also, associated with various other mutations, the abnormal numbers of 16, 20, 22, 23, 24, 27, 28, 29, and 30.

Œnothera gigas is a mutant in which 28 chromosomes, or twice the normal number, appear and, moreover, these chromosomes represent actually twice tho original amount of chromatin material. "Gigas" mutants have been found in various other forms, such as the tomato (Winkler), the jimson weed or *Datura* (Blakeslee and Belling), *Primula* (Gregory) and *Narcissus* (Stomps), and they are always characterized by a doubling of the chromosomes. This condition is termed *tetraploidy* because it shows four times the gametic number of chromosomes.

When a normal diploid *Datura* is crossed with a tetraploid *gigas* individual, a triploid mutant results with a different constellation of somatic characters so that the best of evidence is now at hand that one category of mutations, at least, that of chromosomal

aberrations, is dependent upon, or associated with, abnormal *quantitative* differences in the chromosomes.

The other category of mutations, *factor mutations*, is *qualitative* and concerns the character of hereditary units or genes rather than quantitative groups of these genes as they are assembled in the chromosomes.

Whatever it is that causes the character of a gene to change in quality, with the resultant expression in the somatoplasm, is still apparently beyond the pale of scientific proof. Some investigators find satisfaction in assigning external environmental causes to the solution of the problem while others prefer to conceal their ignorance under the blanket of "internal causes," whatever these may be. At least it is reasonable to say when a new variety appears suddenly in a bottle full of flies or in a field of plants in the same environment with all of its unmodified fellows, that mutation can arise *somehow* without outside interference.

The wild jungle fowl presents a large and useful series of mutations which have cropped out in poultry under the spell of domestication while the goose, on the contrary, although domesticated for an equally long period, has remained practically the same. The *nature* of the plastic hen must be different from that of the more conservative goose.

Meanwhile the secret of the real causes of mutations remains a challenge to every geneticist and success surely awaits some clever workman who knows how to use skilfully the indispensable tools of observation and experimentation.

The bearing of the whole matter of mutation upon

heredity lies in the fact that, contrary to Darwin's belief, it is apparently mutations, and not fluctuations or "modifications," that make up heritable variations. If this supposition proves to be true, mutations furnish the essential material in the study of heredity. Consequently, whatever knowledge we may gain of them has a direct relation to the entire problem of genetics.

CHAPTER IV

THE INHERITANCE OF ACQUIRED CHARACTERS

1. Summary of Preceding Chapters

Hereditary resemblance is due to the derivation of offspring from the same stock as the parent, and successive generations, therefore, are simply periodic expressions of the same continuous stream of germ-plasm.

Perfect inheritance, or uniformity of generations, does not exist, since variations always occur in successive generations. It is upon these variations that evolution depends. Without them there would be no change of type and consequently no possibility of evolutionary advance.

Some variations are fluctuating or continuous in character and may be detected and analyzed by statistical methods, while others are mutations, or discontinuous variations, representing qualitative differences which do not lend themselves readily to statistical analysis.

Mutations are more common than was formerly believed, and since they are germinal rather than somatic in character, they play an important rôle in heredity.

2. The Bearing of this Chapter upon Genetics

Only those variations which reappear in succeeding generations have to do with heredity. Hence it becomes important to inquire as to what kind of variations actually reappear. Can variations that are not inborn, but which are acquired during the lifetime of the individual, be inherited? Does the experience of the parent become a direct part of the child's heritage, or can the environment of the one enter in any way into the heredity of the other? Can changes wrought in the somatoplasm be so impressed upon the germ-plasm as to change it in such a way that it, in turn, will give rise to similarly modified somatoplasm in the next generation? To use Shakespeare's antithesis, can *nurture* as well as *nature* be transmitted? As Conklin says: "Few questions have been discussed so fully and so fruitlessly as this."

In answering these questions we are of course concerned solely with *biological inheritance* and not at all with those extra-biological accumulations in the way of arts, literature, tradition, invention, and the like which constitute civilization and which make us the "heirs of the ages." Such benefits are entailed upon us much in the same way as property is "inherited," but they form no part of the personal biological heritage into which we are now inquiring.

3. The Importance of the Question

This inquiry concerning the inheritance of acquired characters, which Professor Brooks has called "the

interminable question," is not simply an academic matter. Its solution is of vital importance from several viewpoints. For breeders, who are trying to maintain or improve particular strains of animals or plants; for physicians, who, in fighting disease, are honestly seeking to substitute an ounce of prevention for a pound of cure; for sociologists and philanthropists, who have at heart the permanent bettering of human conditions; for educators, who cherish hopes that their life-work of unfolding the youthful mind may prove cumulative and lasting rather than transitory; for religious workers, who want their faith strengthened that conquests in character-building may outreach the individual and so enrich the race; for parents, who entertain hopes that their own efforts may give their children a better biological start in life,—for all these and many more, it is important to know the answer to the question: Can acquired characters be inherited?

4. An Historical Sketch of Opinion

That the personal accumulations of a lifetime are heritable was generally believed throughout the credulous ages. A century ago Lamarck made this idea the corner-stone of his theory of evolution. It was all very simple. The reason evolution occurs in nature is because individual acquirements are being continually added to the onflowing stream of living forms. This cumulation of characters indeed *is* evolution. How else can the present stage of adaptation of organisms

to their several niches in nature be explained save by seeing in it the final results of generations of gradually inherited adaptations?

Darwin also believed in the inheritance of acquired characters, although he differed from Lamarck with respect to how such characters are acquired.

Francis Galton in 1875 was one of the first to express skepticism regarding this generally accepted belief, but the man who, in a masterly manner, focused the growing doubt, and who did more than any other to inspire thought and investigation upon the subject, was August Weismann, who conspicuously bore the torch of genetics between 1880 and 1890. Weismann made the issue so clear that the heritability of acquired characters became the parting of the ways which divided biologists into the two camps of *Neo-Lamarckians* who affirm, and *Neo-Darwinians* who deny, such inheritance. His conclusions, which are the natural outgrowth of the theory of the "continuity of the germplasm," were based, however, upon logical rather than upon experimental grounds.

Comparative anatomists and paleontologists, who are accustomed to work from results back to their causes, are frequently inclined to look favorably upon the inheritance of acquired characters while, on the other hand, geneticists and embryologists, representing the two lines of study which furnish the most immediate approach to this problem, are well-nigh agreed that acquired characters are not inherited. Experiment from cause to result is undoubtedly the best criterion for if the question could be decided by a vote

or by an expression of opinion, the result would be doubtful, since each column contains the names of men whose scientific accomplishments entitle them to a respectful hearing. But just what are the facts of the case?

5. Confusion in Definitions

The source of much of the lack of agreement in this controversy lies in the definition of what constitutes an "acquired character." One is reminded of the two knights who fought so bitterly over the color of a shield, one maintaining that it was red, the other that it was black. So they hacked away at each other, as all good knights should do in the defense of the truth, until they both fell down dead beside the shield which was black on one side and red on the other.

Of course actual characters are never inherited, but only the determiners or potentialities which regulate the way in which the organism reacts to its environment with respect to the characters in question. Reid has pointed out that in one sense every adult character is "acquired" because it has no expression at first. For instance, there is no beard on the face of a male infant, but one will presumably be "acquired" later on in the life-cycle due to a heritable and not to an environmental cause.

It is plain that every new character which represents a forward evolutionary step must have been "acquired," or added, sometime and somewhere, else it would not be present, as there is evidence that it is.

Perhaps the question, as Montgomery has suggested, ought to be changed to read: "*What kinds* of acquired characters are inherited?" It is obvious that discussion is futile until a common denominator in the shape of a definition of acquired characters shall be accepted.

6. Weismann's Conception of Acquired Characters

Weismann defines an acquired character as *any somatic modification that does not have its origin in the germplasm.*

Of course those somatic modifications which are phases of the developing individual, such as the acquisition of a deeper voice at puberty or the substitution of the permanent dentition for the milk-teeth, are somatic variations which have their rise and control in the germplasm and consequently cannot properly be included under the head of acquired characters.

Examples of acquired characters in the Weismannian sense are mutilations, the effects of environment, the results of function as in the use or disuse of certain organs, and such diseases as may be due either to invading bacteria or to the neglect or abuse of the bodily mechanism.

7. The Distinction between Germinal and Somatic Characters

Redfield has thrown light on the classification of the characters which make up the individual by quoting the familiar lines:—

"Some are *born* great,
Some *achieve* greatness,
Some have greatness *thrust* upon them."

"Born" characters are constitutional, having their origin in the germplasm itself. They are never Weismannian acquired characters and may be illustrated by eye-color, mental disposition, or facial features. Lightning calculators and musical prodigies may have their gifts developed and enlarged, but the fact that their talent is nevertheless an unmistakable gift, and not an acquisition, remains true.

"Achieved" characters are functional and are gained by exercise. Many things are achieved, however, which are not acquired characters, as, for instance, wealth, reputation, or an education. Not any of these are biological characters, and therefore we are not concerned with them in this connection, although in the case of education it should be noticed that the mental exercise necessary to bring about a trained mind, if not the subject matter of the education itself, is distinctly an acquired character of the "achieved" type.

"Thrust" characters are the results of environment. They are acquired without functional activity on the part of the organism and usually in spite of anything the organism can do to prevent. Sometimes these characters are thrust upon the individuals before birth, as in the case of blindness caused by parental gonorrhœa or tuberculosis arising from uterine infection, in which case they are termed *congenital* characters.

Congenital or prenatal characters, however, are in

no way the same as germinal characters, for they fall just as truly into the category of acquired variations as do those which make their appearance in later life.

8. What Variations Reappear?

Returning now to Montgomery's question,—"What kinds of acquired characters are inherited?"—it is apparent that only the "born" ones can be, which have their roots in the germplasm whence the new individual arises, and that "achievements" and "thrusts," in order to reappear in the succeeding generation, can do so *only by first becoming incorporated in the germplasm.*

Any character that is not acquired must have been present in the germplasm from which the organism arose, as there is no transfer of characters between organisms except through the germ-cells. Thus it is evident that the only inherited acquisitions are those which, either primarily or secondarily, bring about variation in the germplasm. Such temporary acquisitions as a coat of tan or a display of freckles do not impress the germplasm, for when the cause that incites their appearance is removed, they soon vanish.

9. How may Germplasm acquire New Characters?

In addition to mutation considered in the last chapter, various sorts of rearrangement in the germplasm may present something different.

First may be mentioned the "amphimixis" of Weismann, that is, the mixture of two nearly related strains

of germplasm in sexual reproduction within a species, and secondly, the mixture of two more remotely related strains resulting in hybridization. In either case the strain of germplasm undergoes a shake-up that may result at least in new combinations of characters, if not in the production of entirely new characters. This recombination of characters in amphimixis and hybridization will receive further attention in a later chapter.

The fact that successive parthenogenetic generations, in which amphimixis does not of course occur, may show a larger degree of variability than sexually produced generations, indicates that amphimixis in itself is by no means sufficient to account for all kinds of variations.

It is conceivable that the external factors that act upon the germplasm may be grouped into three classes: —first, external factors acting upon the somatoplasm and then through the agency of the somatoplasm affecting the germplasm ("somatic induction" of Detto or "pangenesis" of Darwin); second, external factors acting directly upon the germplasm and the somatoplasm at the same time ("parallel induction" of Detto); and third, external factors acting upon the germplasm without necessarily at the same time having any effect upon the somatoplasm.

Many instances of direct influence of external factors upon germplasm are known in biological literature, and these have led to some of the misunderstandings concerning the "interminable question" of the inheritance of acquired characters. Sitkowski fed the caterpillars of the moth *Tineola biselliella* with an

aniline dye (Sudan red III), obtaining therefrom, instead of normal whitish ones, moths that laid colored eggs, and these in turn hatched into caterpillars still tinged with the color of the red dye. Riddle, with guinea-pigs, and Gage, with poultry, obtained quite similar results. This case of apparent parallel induction, however, is not a matter of inheritance at all, since the germinal substance itself was not involved, but of animals who got their red color directly from external sources while they were eggs within the mother's body.

10. Weismann's Reasons for doubting the Inheritance of Acquired Characters

Weismann's reasons for questioning the popularly accepted view that acquired characters are inherited may be briefly stated as follows:—

First, there is no known mechanism whereby somatic characters may be transferred to the germ-cells.

Second, the evidence that such a transfer actually does occur is inconclusive and unsatisfactory.

Third, the theory of the continuity of the germ-plasm is sufficient to account for the facts of heredity without assuming the inheritance of acquired somatic characters.

Let us examine these three statements a little more closely.

A. No known mechanism for impressing the germplasm with somatic acquisitions

Each germ-cell remains an independent unit and does not participate in the activities of the body but

lies within the body like a commensal or parasite. It is hard to see, therefore, how a germ-cell can be changed except in a general nutritive way which is quite different from a change in character of any hereditary significance.

The somatoplasm is something that has traveled out from the original fundamental germplasm along the paths of differentiation and elaboration. The more complex the body-cells become, that is, the more successive modifications they undergo, the more difficult it is for these somatic cells to return to their original primitive germinal estate.

In many lower forms of life where cell elaboration is not so great, a part lost by amputation is often regenerated, but this process is not possible in higher forms where the parts represent cell complexes too hopelessly differentiated to begin anew the unfolding sequences of their elaboration. This difficulty was a very real one in the mind of that famous nocturnal inquirer Nicodemus when he asked: "How can a man be born when he is old? Can he enter a second time into his mother's womb and be born?"

Not only the development of the race which we call evolution, but also the determination of the individual in heredity, is a *chain of onward-moving sequences* like the succession of events in history. It is hard to see how recent events can influence preceding events. It is hard to see how the water that has gone over the dam can return and affect the flow of the river upstream in any direct way. It is likewise hard to see how differentiated somatoplasm, which represents the end stage

of a successive series of modifications, can make any definite impress upon the original germplasmal sources from which it arose.

Darwin felt this difficulty and presented with apologies his provisional hypothesis of *pangenesis* in which he assumed that every bodily part sends contributions to the germ-cells in the form of "gemmules." These gemmules, or hypothetical somatic delegates, then reconstruct in the germ-cells the characters of the entire body, including acquired modifications as well as all others, and thus there is no reason why acquired characters cannot readily be transmitted. Unfortunately there is no tangible basis in fact for this delightfully simple explanation to rest upon. It is a theory assuming that *all parental somatic cells* take part in the formation of the new individual, hence it was called "pangenesis," or *origin from all.*

Nothing we have subsequently learned of minute cell structure favors this hypothesis, while many facts go quite against it. Moreover, it is directly opposed to the theory of the continuity of germplasm so convincingly set forth later on by Weismann. Darwin indeed advanced it only in the most tentative way, being entirely ready to see it abandoned at any time for something better. It at least performed one valuable service to science, namely, that of demonstrating how far investigators were from an adequate conception of any means by which somatic modifications might become incorporated in the germ-cells.

We must acknowledge, however, with Lloyd Morgan that the fact that a mechanism for the transfer of

somatic characters to the germ-cells has not been discovered, is not proof that such a mechanism does not exist. It may simply be beyond our present powers of penetration.

B. EVIDENCE FOR TRANSMISSION OF ACQUIRED CHARACTERS INCONCLUSIVE

The evidence for the inheritance of acquired characters was, for a long time, taken for granted. This theory was the most obvious explanation of many facts and so was accepted without question. An obvious interpretation, however, is not always the correct one. The sun appears to go around the earth, but astronomers assure us that it does not.

When Weismann began to sift the evidence for the inheritance of acquired characters, he found that it was largely based upon opinion rather than fact, much like the popular belief with regard to the causation of warts by handling toads.

The supposed evidence for the inheritance of acquired characters falls chiefly into the following categories:—

a. Mutilations;
b. Environmental effects;
c. The effects of use or disuse;
d. The transmission of disease;
e. Immunity;
f. Prenatal influences.

a. Mutilations

It is fortunate that the sons of warriors do not inherit their fathers' honorable scars of battle, else we would now be a race of cripples.

The feet of Chinese women of certain classes have for centuries been mutilated into deformity by bandaging, without the mutilation in any way becoming an inherited character. The same result is also true of tattooing and of circumcision, the latter a mutilation practised from ancient times by the Jews and certain other Eastern peoples. The progressive degeneration or crippling of the little toe in man has been explained as the inheritance of the cramping effect of shoes upon generations of shoe wearers, but, as Wiedersheim has pointed out, the fact that Egyptian mummies show the same crippling of the little toe is unfavorable to this hypothesis, for no ancient Egyptian could ever be accused of wearing shoes or of having had shoe-wearing ancestors. Sheep and horses with docked tails as well as dogs with trimmed ears never produce young having the parental mutilation.

Weismann's classic experiment with mice, an experiment subsequently confirmed by others, is additional negative evidence upon this same point. What Weismann did was to breed mice whose tails had been cut off short at birth. He continued this decaudalization through twenty-two generations with absolutely no effect upon the tail-length of the new-born mice. One may see in the catacombs of the Zoologisches Institut at Freiburg, filed carefully away on shelves,

as a "document," long rows of labeled bottles containing the fifteen hundred and ninety-two martyrs to science which made up the twenty-two generations of mice in this famous experiment.

Blaringhem, it is true, obtained mutations which bred true from latent buds that were forced into development following mutilation of normal buds, but Griffon has shown that similar mutations occur without preceding mutilations so that this, as Shull points out, is simply a case of segregation of biotypes already present in the mutilated parent.

Conklin has hit the nail upon the head with respect to mutilations by saying: "Wooden legs are not inherited, but wooden heads are."

b. Environmental Effects

Trees deformed by prevailing winds, like the willows that line the canals in Belgium and Holland, or storm-crippled trees along the exposed seacoast are not known to produce a modified progeny when their adverse environmental conditions are removed. Similarly, the persistent sunburn of Englishmen long resident in India does not reappear in their children born in England.

Sumner kept mice in a constant but abnormally high temperature of 26° C. with the result that the ears, tail, and feet grew noticeably larger than in control animals kept in ordinary lower temperatures, while at the same time the general hairiness of the body decreased. It should be remembered, however, that mice

are mammals which pass through an extended uterine existence, so that it is easy to see how the offspring in this case were subjected to the same excessive temperature as the parents for a period sufficient to amply account for their subsequent variation when removed to a normal environment.

Zederbaur finds that the wayside weed *Capsella*, which in the course of many years has gradually crept along the roadsides up into an Alpine habitat and there "acquired" Alpine characters, upon being transplanted to the lowlands retains its Alpine modifications. Although this case has been cited as an authentic instance of the inheritance of acquired characters, is it not possible that the conquest of the Alps by *Capsella* has been due, in the course of time, not to the inheritance of acquired characters at all, but to a gradual natural selection of just those germinal variations which best fitted it to cope with Alpine conditions until, finally, a strain of germplasm producing somatoplasm suitable to Alpine conditions has been isolated in the form of an elementary species derived from the original type? If this is what has happened, of course such germplasm would give rise to Alpine plants whether individual plants grew to maturity near the snow-line or in the warm valleys at a lower altitude.

Kammerer, by reducing the water supply, succeeded in transforming *Salamandra maculosa*, a salamander normally producing about seventy eggs which, when hatched in water, become gill-breathing tadpoles, into a salamander producing only two to seven young which are born alive without gills and are able to live

out of water entirely, in damp situations. These land-adapted offspring, moreover, when supplied with abundant water, produce in turn tadpoles which spend days only, instead of months, in the water undergoing their metamorphosis, thus showing an apparent inheritance of an acquired character.

It should be pointed out, however, that in these cases the gill-breathing forms in each instance represent a case of arrested development. *Axolotl* is simply a larval form of *Amblystoma* which, under normal conditions of an abundant water environment and high temperature, gets no further in its metamorphosis than the tadpole stage, when it produces eggs and sperms and finishes its life story. A change in environment simply permits the life-cycle to go on further. Changing from gill-breathing to lung-breathing is not, therefore, an acquired character, but a purely germinal character that may be either blocked or released by changing conditions in the environment. The phenomenon is termed *neotony.*

c. *The Effects of Use or Disuse*

The callosities on the end of a violinist's left-hand fingers are acquired by use, but they are not inherited. There are callosities on the knees of the wart-hog, *Phacochœrus,* which are also apparently the result of use, for these animals kneel as they root for a living in the African forests, and have done so for untold generations. It has been noticed that young wart-hogs as soon as they are born possess the callosities, so that

this instance looks like one of inheritance of a character acquired through use or exercise.

The skin on the soles of human feet is thicker than the skin elsewhere, and by use it becomes still thicker. This is apparently another instance of the same sort. The writer has observed, however, that a cross section through the foot of a "mud puppy," *Necturus maculatus*, shows a much thickened sole. *Necturus*, it should be noted, is a very primitive salamander living always under water and never using the soles of its feet in any way to bear its weight, nor is it reasonable to suppose that it ever had any ancestors who did so, for the hands and feet of the Amphibia are the most primitive and ancient hands and feet to be found in the animal kingdom without any known ancestral types. The thickening of the skin on the sole of the mud puppy's feet must be due, therefore, to germinal determiners and is in no way an acquisition through use. The same may also be true of the wart-hog's knees and of human soles.

The strong arm, the skilled hand, and the trained ear are not inherited. They have always to be reacquired in each succeeding generation just as surely as the ability to walk, or to read and write.

Herbert Spencer has defined instinct as "inherited habit." But surely those instincts which determine a single isolated action during the lifetime of the individual, such as the spinning of a peculiar cocoon, cannot be the result of habit, since habits are formed only through repeated action.

Dr. Hodge, who succeeded in hatching tame quail

chicks out of "wild" eggs, asks the pertinent question: "How can a *fear* hatch out of an egg?" The habit of wildness, particularly with precocial chicks like quails, may, under an inciting environment, be very soon established but it is difficult to see how caution, gained by the experience of the parents, can find its way into the fertilized egg. If, then, *some* instincts require a different explanation from that of "inherited habit," may it not be likely that all instincts do? Is it not better to assume that the structure of the germ-plasm determines a particular response to a particular stimulus regardless of whether in the past the ancestors have made a similar response to a similar stimulus?

d. Transmission of Disease

If acquired diseases were heritable we would all have been dead long ago. When a son, whose father died of pneumonia, succumbs himself to pneumonia after an interval of years there may be no more causal or hereditary connection between the two events than when a second house burns down on the same site where a former house went up in flames.

Many diseases, like tuberculosis, have their immediate cause in invading pathogenic bacteria. Bacteria themselves cannot be inherited for the reason that it is not possible for them to become an integral part of the fertilized egg and thus cross the "hereditary bridge" which joins two generations. A general predisposition to bacterial disease, that is, a lack of resistance to bacterial invasion due to defectiveness in

physical or physiological equipment, may be present as a combination of characters in the germplasm, or an individual, as the result of disease, may "acquire" a generally weakened germplasm and so produce a progeny exhibiting general liability to disease; but it is doubtful if such a condition can properly be termed the inheritance of an acquired character, since the particular definite disease in question is not demonstrably heritable.

When alcoholism "runs in a family," its reappearance in the son is probably due to the fact that he is derived from the same weak strain of germplasm as his father. The fact that the father succumbed to the alcohol habit is not the determining cause of drunkenness in the son. The same thing that caused the father to become an alcoholic, namely, weak germplasm, and not the resulting drunkenness in the parent, is the causal factor for alcoholism in the son.

At the same time it is entirely probable that hereditary alcoholism may in some cases arise through "parallel induction," that is to say, acquired alcoholism may end in the simultaneous poisoning and consequent modification of both the somatoplasm and germplasm of the parent, with the result that the germplasm has less resistance to alcoholism in a succeeding generation. The offspring are consequently more likely to succumb to the disease. This, however, is not the inheritance of an acquired character or of a definite somatic modification.

When a man of the present generation has rheumatic gout, it is a severe stretch both of patriotism

and of the powers of heredity to trace the origin of the affliction back to a revolutionary ancestor who acquired sciatic rheumatism by sleeping on the ground at Valley Forge, yet this is quite as direct as many alleged instances of the inheritance of disease.

In the majority of instances, apparent cases of the inheritance of disease are merely instances of *reinfection.* This reinfection of the offspring may occur very early in embryonic life, even in the egg, in the case of pebrine in silkworms (Pasteur) and in the tick which transfers the protozoan parasite causing Texas fever. Or it may happen after birth, provided the offspring are exposed to the same environment as that in which the parent acquired the disease, but in any case *reinfection is not heredity.*

e. Immunity and the Effect of Drugs

Ehrlich subjected mice to increasing doses of ricin until they became immune to doses which are ordinarily fatal. When these ricin-immune mice were bred to non-immune mates the offspring in turn showed some degree of immunity *if the immunized parent was a female* but not if the immunized parent was a male. In other words, the immunity was transferred through the female only, where the blood of the mother is for a considerable period during fœtal life in intimate relation with the blood of the offspring. Even here, just as in the lifetime of an immunized individual, the immunity tended to fade out after a short time.

As a matter of fact many of the instances that have

been advanced to show the inheritance of acquired characters are simply transient hold-over somatic effects that have gained no permanent grip upon the hereditary stream of germplasm, and which consequently soon fade away.

In a similar way the gradual acclimatization of the mold, *Penicillium*, to a salt solution of a density sufficient to cause its death if placed in it at once, has been effected, and the resulting spores have produced molds that are able to survive in the concentrated solution. Here, of course, the spores have been acclimatized as well as the parent plant and it was to be expected that these spores would develop into molds habituated to the increased saline environment. This, however, is pseudo-heredity, for no permanent method of response has been established.

f. Prenatal Influences

Perhaps the most illogical and at the same time the most widespread of all types of supposed transmission of acquired characters are the so-called "maternal impressions." The prevalence of this superstition has caused expectant mothers untold needless misery.

Popenoe and Johnson, after an excellent and extended discussion of the matter, conclude as follows:—

"To recapitulate, the facts are—

(1) That there is, before birth, no connection between the mother and child, by which impressions on the mother's mind or body could be transmitted to the child's mind or body.

(2) That in most cases the marks or defects whose origin is attributed to maternal impression, must necessarily have been complete long before the incident occurred which the mother, after the child's birth, ascribes as the cause.

(3) That these phenomena usually do not occur when they are, and by hypothesis ought to be, expected. The explanations are found after the event, and that is regarded as causation which is really coincidence.

. . . .

It is easily understandable that any event which makes such an impression on the mother as to affect her health, might so disturb the normal functioning of her body that her child would be badly nourished, or even poisoned. Such facts undoubtedly form the basis on which the airy fabric of prenatal culture was reared by those who lived before the days of scientific biology."

C. THE GERMPLASM THEORY SUFFICIENT TO ACCOUNT FOR THE FACTS OF HEREDITY

Weismann holds that the theory of the continuity of the germplasm, already considered in a previous chapter, is sufficient in itself to account for the facts of heredity. Hence it is quite unnecessary to fall back upon the inheritance of acquired characters as an explanation, since this theory is at least difficult, if not impossible, of satisfactory proof.

To prove the inheritance of acquired characters, according to Weismann three things are necessary: *first*, a particular somatic character must be called

forth by a known external cause; *second*, it must be something new or different from what was already exhibited before, and not be simply the reawakening of a latent germinal character; and *third*, the same particular character must reappear in succeeding generations in the absence of the original external cause which brought forth the character in question. As yet these conditions have not been convincingly met in the evidence which has been brought forward in support of the inheritance of acquired characters.

11. The Comparative Independence of Germ and Soma

The fact that the germ is only a pilgrim stranger passing through the homeless land of the soma is well brought out by the critical ovarian transplantation experiments of Castle and Phillips upon guinea-pigs. The ovaries of an albino guinea-pig were removed and those of a black guinea-pig were grafted in their place. After recovery from the operation the animal was mated with an albino male three times before pneumonia unfortunately put an end to this famous experiment. The resulting offspring were all black, as shown in Figure 12. Ordinarily when albinos are crossed they produce only albinos. It is obvious that the pneumonia victim was not the mother of the six black offspring although she bore them. "The conclusion is forced upon us," to quote Babcock and Clausen's comments on the case, "that the egg-cell during its growth does not change in germinal constitution. Its growth is like the growth of a parasite or of a wholly

independent organism; what it takes up serves as food; this is not incorporated merely in the growing organism, it is *made over* into the same kind of living substance as composes the assimilating organism."

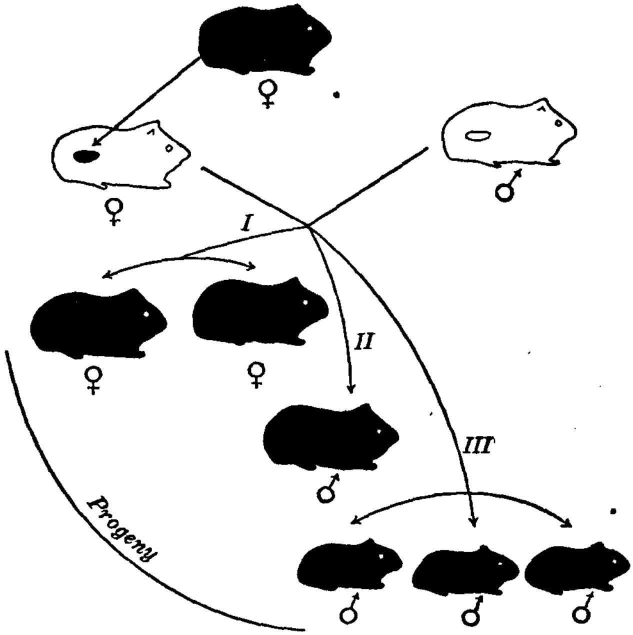


FIG. 12.—Diagram of ovarian transplantation experiment to show the influence of somatoplasm upon germplasm. Black is dominant over albino. The ovaries from a black guinea-pig were engrafted into a female albino whose ovaries had been removed. Upon recovery this female was crossed three times with an albino male. All the progeny were black. Data from Castle and Phillips.

12. ACQUIRED CHARACTERS IN THE PROTOZOA

Although the problem of the inheritance of acquired characters is much better defined among the higher ani-

mals where the distinction between the soma and the germ is more sharply cut than among the lower animals and plants, yet, as Jennings points out, one meets

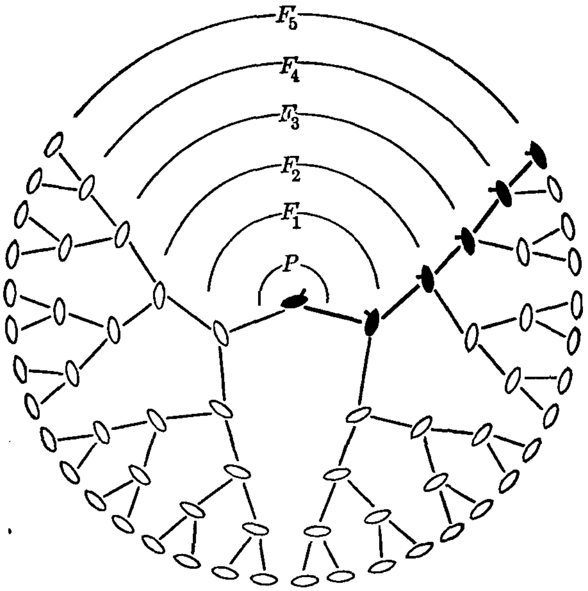


FIG. 13.—The behavior of an "acquired character,"—a spiny projection at one end of the body,—in the case of *Paramecium.* The original individual is represented in the center and its offspring, which arise by fission, are in successive circles. In the fifth generation only one out of 32 shows the spine. Data from Jennings.

the same difficulties in the protozoa as in the metazoa. The difficulty in the inheritance of acquired characters is not so much in separating germ and soma as in the mechanism of cell-division. There seems to be no way in which an acquisition located at one end of a

cell can overleap the barrier of cell division and appear at the other end after mitosis.

In his cultures Jennings found a *Paramecium* with an abnormal spine at one end. This acquisition was handed on for five generations before it disappeared but never in any generation did more than one of the offspring have the spine. In other words, it did not become hereditary although it continually reappeared in one individual in every generation. The reason for this will be apparent upon referring to Figure 13. The fission-half bearing the spine holds the same relation to the spineless half as soma to germ and there is here no mechanism for the transmission from one half to the other. Simple transmission, like the persistence of the spine for five generations of *Paramecium* is not heredity. In order that a character shall be really inherited, that is, shall appear in more than one of the progeny and so affect the race, it must be *produced anew in each generation from a germinal determiner.* This is just as true for the protozoa as it is for the higher organisms.

13. The Opposition to Weismann

The opponents of Weismann point out, as a weak place in his argument, the assumption that the germplasm is so insulated from the somatoplasm as not to be influenced by it. Weismann assumes, of course, that the germplasm is isolated from the somatoplasm very early in the development of the fertilized egg into an individual, and that when once isolated it thereafter

takes no active part in, nor is in any way affected by, the vicissitudes through which the somatoplasm, or the body itself, passes. The somatoplasm is thus merely a carrier of the germplasm and unable to affect the character of it any more than a rubber hot-water bag, although capable of assuming a variety of shapes, can affect the character of the water within it.

In opposition to this view it is urged that every organism is a physiological as well as a morphological unity, and that cells entirely insulated within such a unity would be a physiological miracle.

There is abundant evidence that germ-cells, or rather the hormones in the sexual organs producing the germ-cells, do affect the somatoplasm under particular conditions, as, for example, in cases of castration when those somatic features called "secondary sexual characters" undergo profound modification.

Even here, however, it must be pointed out that it is not the germ-cells themselves that are directly responsible for the modifications which occur, but rather the hormones of the interstitial gonadal cells. A most serious fly in the Weismannian ointment is due to the results of certain recent experiments by Guyer and Smith.[1] These ingenious experimenters injected into fowls the freshly removed lenses of rabbits' eyes that had been pulped up in Ringer's solution. The fowls developed an "anti-body" which tended to dissolve and disintegrate the rabbit lenses. When serum from these fowls was in turn injected into pregnant rabbits the mother was unaffected but nine out of sixty-

[1] *Jour. Exp. Zool.* III, 1920.

one surviving young were born with degenerate eyes. The affected young have carried the defect even in the male line through eight generations without the injection of any more serum containing the lens anti-body. "The degenerating eyes are themselves, directly or indirectly, originating anti-bodies in the blood serum of their bearers—which in turn affect the germ-cells." If these conclusions are substantiated, the cardinal principle of the inheritance of acquired characters is conceded. The end is not yet!

14. Various Results upon Offspring of Parental Acquisitions

In Diagram 14 an attempt is made to visualize the various results of parental acquisitions, both somatic and germinal, upon the generations following.

It will be noted that Case I, where the soma of the parent is represented as determining the soma of the offspring, is contrary to fact for in sexual reproduction the offspring arises from the undifferentiated germplasm of its parents.

The usual result of a somatic modification is shown in Case II.

Pangenesis, Case III, postulates a reversal of the universal process of differentiation in that it demands a return of the elaborated soma with the modifications it has acquired during the course of its elaboration, to the primitive condition of the germ.

In Case IV the apparent inheritance of acquired characters is due not to the fact that the parental soma

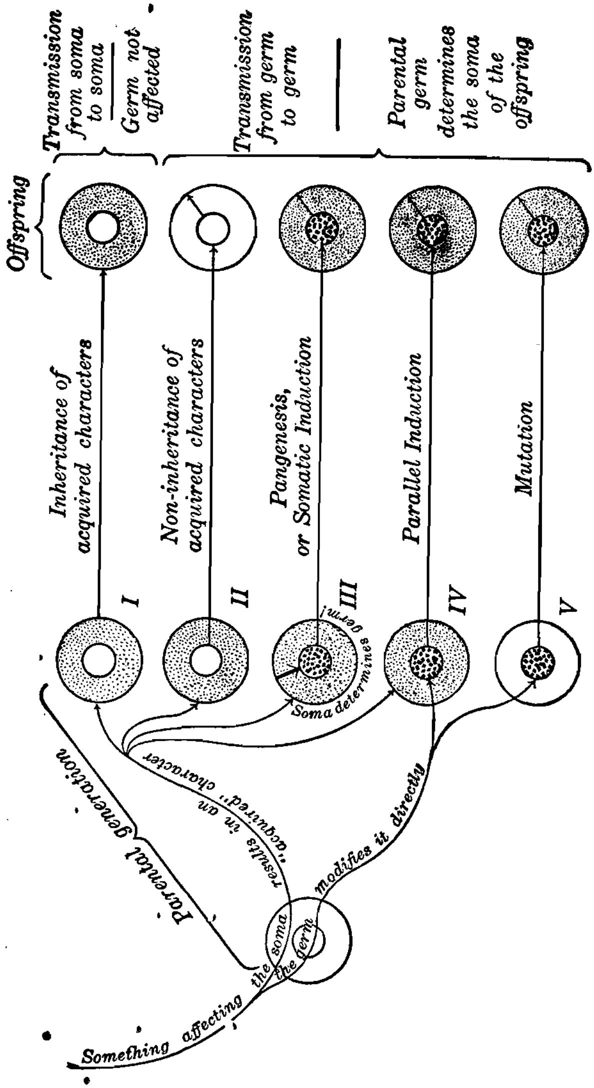


FIG. 14.—The theoretical results in the offspring, of parental acquisitions.

was modified, but because at the same time and in the same way that the parental soma was taking on a modification, the germ was likewise modified. This, to use the drug clerk's phraseology, is "something just as good" as the inheritance of acquired characters but it is not the Weismannian brand.

Finally, Case V shows a true mutation which occurs in the parental germplasm but does not appear to the light of day until the offspring develops.

15. Conclusion

But even granting that the somatoplasm affects the germ-cells, the inheritance of acquired characters is by no means thereby established.

In order to do this, the precise acquired character *in question, which indirectly exercised its influence* upon the germ, must be redeveloped, and, although the germplasm might conceivably receive an influence from the somatoplasm and be affected by it in a general way, it is a different matter entirely to develop anew the replica of the character itself which is supposed to have been acquired.

It will be seen in subsequent pages, under the discussion of data furnished by experimental breeding, that the weight of probability is decidedly against the time-honored belief in the inheritance of acquired characters.

CHAPTER V

MENDELISM

1. Methods of Studying Heredity

Modern studies in heredity have been pursued principally in three directions: first, by microscopical examination of the germ-cells; second, by statistical consideration of data bearing upon heredity; and third, by experimental breeding of animals and plants. In the present chapter attention will be directed to a consideration of experimental breeding with reference to hybridization, that is, breeding from unlike parents, a process which Jennings characterizes by the expressive phrase, "the melting-pot of cross-breeding."

2. The Melting-pot of Cross-breeding

Hybridization, or cross-breeding, as analyzed by Galton (1888), results in one of three kinds of inheritance, namely, blending, alternative, or particulate.

Of these, *blending inheritance* may be called the typical "melting-pot" in which contributions from the two parents fuse into something intermediate and different from that which was present in either parent. Galton illustrated this process by the inheritance of human stature in which a tall and a short parent pro-

duce offspring intermediate in height. A more thorough consideration of this type of inheritance will be presented in Chapter VIII.

By the method of *alternative inheritance* the parental contributions do not melt upon union, but retain their individuality, reappearing intact in the off-

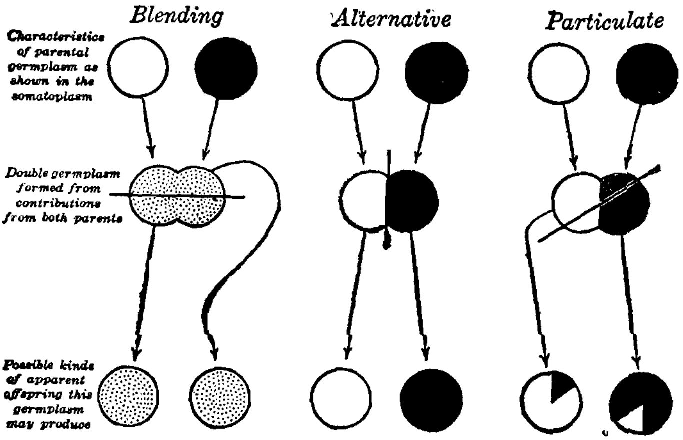


FIG. 15.—Three kinds of inheritance described by Galton, when applied to a single pair of characters.

spring. In inheritance of human eye-color, for example, the offspring usually have eyes colored like those of one of the parents when the parental eye-color is unlike in the two cases, rather than eyes intermediate in color between those of both parents.

Particulate inheritance results when the offspring present a mosaic of the parental characters, that is, when parts of both the maternal and paternal characters reappear in the offspring without losing their iden-

tities by blending or without excluding one another. Piebald races of mice arising from parents with solid but different colors have been cited as illustrations of this sort of inheritance, although it will be seen later in connection with the "factor hypothesis" that another interpretation of this phenomenon is not only possible but probable.

The distinctions between these three categories of inheritance are diagrammatically represented in Figure 15.

3. Johann Gregor Mendel

Our understanding of the working of inheritance in hybridization we owe largely to the unpretentious studies of an Austrian monk, Johann Gregor Mendel, who, although a contemporary of Darwin, was probably unknown to him. Bateson says of Mendel: "Untroubled by any itch to make potatoes larger or bread cheaper he set himself in the quiet of a cloister garden to find out the laws of hybridity, and so struck a mine of truth, inexhaustible in brilliancy and profit." For eight years Mendel carried on original experiments by breeding peas and then sent the results of his work to a former teacher, the celebrated Karl Nägeli, of the University of Vienna. At the time Nägeli's head was full of other matters, so that he failed to see the significance of his old pupil's efforts. However, in 1866 Mendel's results appeared in the Transactions of the Natural History Society of Brünn,[1] an obscure publication

[1] Verhandlungen naturf. Verein in Brünn. Abhandl. IV, 1865 (which appeared in 1866).

that reached hardly more than a local public. Here Mendel's investigations were buried, so to speak, because the time was not ripe for a general appreciation or evaluation of his work.

At that time neither the chromosome theory nor the germplasm theory had been formulated. Moreover, much of our present knowledge of cell structure and behavior was not even in existence. Weismann had not yet led out the biological children of Israel through the wilderness upon that notable pilgrimage of fruitful controversy which occupied the last two decades of the nineteenth century, and the attention of the entire thinking world was being monopolized by the newly published epoch-making work of Charles Darwin.

Mendel died in 1884, and his work slumbered on until it was independently discovered, almost simultaneously, by three botanists whose researches had been leading up to conclusions very much like his own. These three men were deVries of Holland, von Tschermak of Austria, and Correns of Germany. Their contributions were published only a few months apart in 1900 and were closely followed by important papers from Bateson in England, Cuénot in France and Davenport and Castle in America, extending Mendelism to animals, with a rapidly increasing number from other biologists the world over. To-day the literature upon this subject has grown to be very large, and the end is by no means yet in sight.

Castle has well said: "Mendel had an analytical mind of the first order which enabled him to plan and carry through successfully the most original and instructive series of studies in heredity ever executed."

4. Mendel's Experiments on Garden Peas

What Mendel did was to hybridize certain varieties of garden peas and keep an *exact record of all the progeny*, in itself a simple process but one that had never been faithfully carried out by any one.

"To Mendel's foresight in arranging the conditions of his work, as much as to his astuteness in interpreting the data, is due his remarkable success." (Morgan.)

Before examining Mendel's results it may be well to state the difference between normal and artificial self-fertilization. Self-fertilization occurs when from the pollen and ovule of the same flower are derived the two gametes which uniting produce a zygote that develops into the seed and subsequently into the adult plant of the next generation. In artificially crossing normally self-fertilized flowers it is necessary to carefully remove the stamens from one flower while its pollen is still immature, and later, at the proper time, to transfer to it ripe pollen from another flower.

Mendel's cross-breeding experiments on peas showed certain numerical relations among the progeny which gave rise to what has come to be rather indefinitely known as "Mendel's law." This law may be temporarily formulated as follows:—

When parents that are unlike with respect to any character are crossed, the progeny of the first generation will apparently be like one of the parents with respect to the character in question. The parent which impresses its character upon the offspring in this manner is called the *dominant*. When, however, the hybrid offspring of this first generation are in turn

crossed with each other, they will produce a mixed progeny, 25 per cent of which will be like the dominant grandparent, 25 per cent like the other grandparent, and 50 per cent like the parents resembling the dominant grandparent.

An illustration will serve to make plain the manner in which this law works out.

Mendel found that when peas of a tall variety were artificially crossed with those of a dwarf variety, all the resulting offspring were tall like the first parent. It made no difference which parent was selected as the tall one. The result was the same in either case, showing that the character of tallness is independent of the character of sex.

When these tall cross-bred offspring were subsequently crossed with each other, or allowed to produce offspring by self-fertilization which amounts to the same thing, 787 plants of the tall variety and 277 of the dwarf kind were obtained, making approximately the proportion of 3 to 1.

On further breeding the dwarf peas thus derived proved to be pure, producing only dwarf peas, while the tall ones were of two kinds, one third of them "pure," breeding true like their tall grandparent, and two thirds of them "hybrid," giving in turn the proportion of three tall to one dwarf like their parents.

These crosses may be expressed as follows:—

$$\text{Tall, } T, \times \text{ dwarf, } t, = \text{ tall, } T(t).$$

That is, tallness crossed with dwarfness equals tallness with the dwarf character present but latent.

Mendel termed the character, which became apparent in such a hybrid, in this case tallness, the *dominant*, and the latent character which receded from view, in this instance dwarfness, the *recessive*.

The members of such a Mendelian pair are termed *allelomorphs*.

When now the hybrids, $T(t)$, were crossed together, the result algebraically expressed was as follows:—

$$\begin{array}{l} \quad T + t \text{ (all possible egg characters)} \\ \quad \underline{T + t \text{ (all possible sperm characters)}} \\ TT + Tt \\ \qquad\quad Tt + tt \\ TT + 2\,T(t) + tt \end{array}$$

That is, one of the four possible cases was dwarf, *tt*, in character and the other three were apparently tall, although only one out of the three was pure tall, *TT*, while the remaining two were tall with the dwarf character latent, $T(t)$.

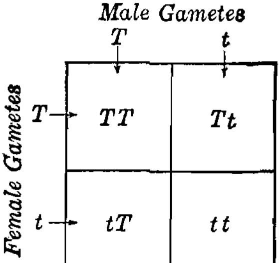


FIG. 16.—Diagram to illustrate theoretically the formation of the four possible zygotes in the second filial generation of a monohybrid.

The same thing may be expressed more graphically by the checkerboard plan, which Punnett suggested (Fig. 16). Each square of the checkerboard represents a zygote which, having received a gamete from each of the two parents, may develop into a possible offspring. The character of the gametes of the parents is shown out-

side of these squares, while the arrows represent the parental source from which the offspring have received their hereditary composition.

The essential feature of Mendel's law is briefly this: *hereditary characters are usually independent units which segregate out upon crossing, regardless of temporary dominance.*

Mendel carried on further experiments with garden peas, using other characters. He obtained practically the same result as in the instance already given, for the actual progeny in the second generation of the cross-bred offspring figured up, as seen in the table below, very nearly to the expected theoretical ratio of 3 to 1.

Character	Number of Dominants	Number of Recessives	Ratio
Form of seed . . .	5474 smooth	1850 wrinkled	2.96 to 1
Color of seed coat . .	6022 yellow	2001 green	3.01 to 1
Length of stem . . .	787 tall	277 dwarf	2.84 to 1
Color of flowers . .	705 colored	224 white	3.15 to 1
Position of flowers .	651 axial	207 terminal	3.14 to 1
Form of pods . . .	882 inflated	299 constricted	2.95 to 1
Color of unripe pods .	428 green	152 yellow	2.82 to 1
Total	14949	5010	2.98 to 1

These results have been confirmed by other investigators, for example the yellow-green seed-color cross has been repeated by Correns, Tschermak, Hurst, Bateson, Lock, Darbishire and White, with results totalling 195,477 in the second generation of which number 146,802 were yellow and 48,675 were green. This is a proportion of 3,016 to 1.

5. Some Further Instances of "Mendel's Law"

Since the rediscovery of Mendel's law the ratio of 3 to 1 in the second hybrid generation has been found by a number of different investigators to be constant in a large array of characters observed both in animals and plants of diverse kinds when these are cross-bred with reference to the characters in question.

Botanists have an advantage perhaps in this matter, as they deal with forms which usually produce a large number of offspring from a single cross, a very desirable condition in estimating ratios. On the other hand, they are handicapped by being unable usually to obtain more than one generation in a year, while zoologists may secure from animals like rabbits and mice several generations in a year, although ordinarily the number of progeny is much smaller and the ratios obtained have a larger chance of error than is the case with the more numerous plant offspring.

Semi-microscopic animals, as, for example, the pomace fly, *Drosophila*, which produces a large progeny every two weeks or so, may combine the general advantages mentioned for the two groups of organisms indicated above, but they have the disadvantage of being so small that the detection of their distinctive phenotypic characters is attended with considerable technical difficulty.

What the modern experimenter in genetics desires is an organism, first, which possesses conspicuous distinctive somatic characters, and, second, that will come to sexual maturity early and breed either in captivity or

under cultivation both numerously and frequently with a minimum of trouble and expense.

The following table, compiled chiefly from Bateson [1] and Baur,[2] might easily be much extended. It shows

Organism	Author	Date	Dominant	Recessive
Nettles	Correns	'03	Serrated leaves	Smooth-margined leaves
Sunflower	Shull	'08	Branched habit	Unbranched habit
Cotton	Balls	'07	Colored lint	White lint
Snapdragon	Baur	'10	Red flowers	Non-red flowers
Wheat	Biffen	'05	Susceptibility to rust	Immunity to rust
Tomato	Price and Drinkard	'08	Two-celled fruit	Many-celled fruit
Maize	deVries	'00	Round, starchy kernel	Wrinkled, sugary kernel
Silkworm	Toyama	'06	Yellow cocoon	White cocoon
Cattle	Spillman	'06	Hornlessness	Horns
Pomace fly	Morgan	'10	Red eyes	White eyes
Horses	Bateson	'07	Trotting habit	Pacing habit
Land snail	Lang	'09	Unbanded shell	Banded shell
Mice	Darbishire	'02	Normal habit	Waltzing habit
Guinea-pig	Castle	'03	Short hair	Angora hair
Canaries	Bateson and Saunders	'02	Crest	Plain head
Poultry	Davenport	'06	Rumplessness	Long tail
Man	Farrabee	'05	Brachydactyly	Normal joints
Barley	von Tschermak	'01	Beardlessness	Beardedness
Salamander (Amblystoma)	Haecker	'08	Dark color	Light color

from what diverse sources confirmatory evidence of the truth of Mendel's law has been derived within the first ten years of observation and experiment after its rediscovery.

[1] "Mendel's Principles of Heredity," 1909.
[2] "Einführung in die experimentelle Vererbungslehre," 1911.

6. The Cardinal Principle of Segregation

The essential thing which Mendel demonstrated was the fact that, in certain cases at least, the determiners of heredity derived from diverse parental sources may unite in a common stream of germplasm from which, in subsequent generations, they may segregate out apparently unmodified by having been intimately associated with each other. This *law of segregation*, or "independent assortment" as Morgan prefers to call it, depends upon the conception that the individual is made up of a bundle of unit characters. It may be illustrated by the separate flowers picked from a garden which, after being made into a nosegay, may be taken apart and rearranged without in any way disturbing the identity of the separate blossoms.

The general formula of segregation that covers all cases of organisms cross-bred with respect to a single character, that is, *monohybrids*, is given in Figure 17.

The parents of a hybrid are usually referred to as the *parental generation* (P). The hybrid generation formed by crossing diverse characters in parents is designated as the *first filial generation* (F_1). The offspring of F_1 are F_2, and so on.

Incidentally this diagram hints how it is possible to derive a pure strain from an impure (hybrid) source, a fact of immediate interest not only to breeders of animals and plants but also to breeders of men.

Such "extracted" recessives or dominants will be entirely free of the hybrid impurity.

7. Definitions

A character which is present in the offspring in double quantity because it was present in both parents is said by Bateson to be *homozygous*, while an organism which is homozygous with respect to any char-

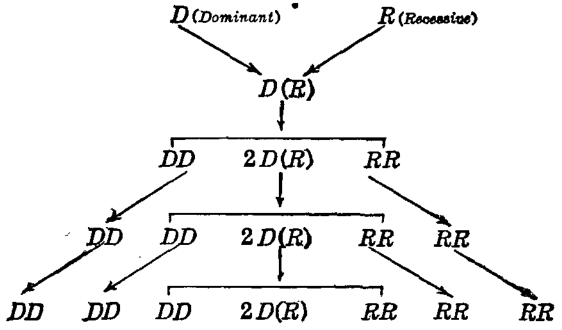


Fig. 17.—General Mendelian formula for a monohybrid

acter is called a *homozygote* so far as that partic character is concerned (DD or RR.)

In contrast to the homozygous condition, an organism is said to be *heterozygous* when it derives the determiner of a character from only one parent. Such an organism is described as a *heterozygote* with respect to the character in question (DR).

Organisms that appear to be alike, regardless of their germinal constitution, are said by Johannsen to be identical *phenotypically* (DD and DR), while organisms having identical germinal determiners are said to be *genotypically* alike (DD and DD or RR and RR).

The word "genotype" was suggested by Johannsen in honor of Darwin and his theory of pan*gen*esis, although there are certain objections to its use in this connection for the reason that systematists have already appropriated it in a different sense. As here used it signifies "the fundamental hereditary constitution or combination of genes of an organism" (Shull).

8. The Identification of a Heterozygote

"Homozygote" and "heterozygote" are terms then descriptive solely of the genotypical constitution of organisms, and, as has been said, it is not always possible to distinguish one from the other by inspection. *The only sure way to identify a heterozygote is by breeding to a recessive and observing the kind of offspring produced.*

Peas of the formulæ TT and $T(t)$, for example, both look alike, since a single determiner for the tall character, T, is sufficient to produce complete tallness. When, however, these two kinds of tall peas are each bred to a recessive dwarf pea, of the formula tt, the progeny will differ distinctly in the two cases as follows:—

Case I. $T + T \times t + t = 100$ per cent $T(t)$.
Case II. $T + t \times t + t = 50$ per cent $T(t) + 50$ per cent tt.

That is, if the dominant to be tested is homozygous (Case I), the entire progeny will exhibit the dominant character, but if the dominant to be tested is heterozygous (Case II), then only one half of the progeny will show the character in question.

Sometimes when dominance is not pronounced it is possible to distinguish the heterozygote dominant from the homozygote dominant. Correns has described an excellent instance of this type. When plants of a white-flowering race of the four-o'clock, *Mirabilis jalapa*, are crossed with those of a red-flowering race, all the offspring in the first filial generation, unlike either parent, exhibit rose-colored flowers. When, however, these rose-colored flowers are crossed with each other, they produce red, rose, and white in the Mendelian ratio of 1 : 2 : 1; that is, three colored to one white. The red-flowering race thus proves to be homozygous and the rose-flowering race heterozygous. Here color dominates the absence of color, or white, but the *degree* of the color depends upon whether the dose of pigment is double, from both parents, or single, from only one parent.

9. The "Presence or Absence" Hypothesis

In place of Mendel's conception that every dominant character is paired with a recessive alternative or *allelomorph*, there has been proposed *the presence or absence hypothesis* which was first suggested by Correns but later logically worked out by others, particularly by Hurst, Bateson, and Shull. According to this interpretation, a determiner for any character either is, or is not, present. When it is present in two parents, then the offspring receive a double, or *duplex*, "dose," to use Hurst's word, of the determiner. When it is present in only one parent, then the offspring have

a single, or *simplex*, dose of the character. When it is present in neither parent, it follows that it will not appear in the offspring. In this case the offspring are said to be *nulliplex* with respect to the character in question. Take the case of tall and dwarf peas, the determiner for tallness when present produces tall peas, even if it comes from only one parent, but if this determiner for tallness is absent from both parents, the offspring are nulliplex, that is, the absence of tallness results and only dwarf peas are produced.

The difference between the presence or absence theory and the dominant or recessive theory of allelomorphs is that in the former case the "recessive" character has no existence at all, while in the latter instance it is present, but in a latent condition.

The reasons for and against the presence or absence interpretation may be more suitably considered later.

10. Dihybrids

So far reference has been made exclusively to *monohybrids*, any two of which are supposed to be similar except with respect to a single unit character. Monohybrids are comparatively simple, but when two organisms are crossed which differ from each other with respect to *two* different unit characters, the situation becomes more complicated.

Mendel solved the problem of dihybrids by crossing wrinkled-green peas with smooth-yellow peas. He found that *smoothness*, *S*, is dominant over *wrinkledness*, *W*, and that *yellow color*, *Y*, is dominant over *green*, *G*,

or, as it would be stated according to the presence or absence theory, smoothness is a positive character which fills out the seed-coat to plumpness while its absence leaves a wrinkled coat, and yellowness is a positive character due to a fading of the green which causes the yellow to be apparent. In the absence of this green-fading factor, or determiner, the green of course appears.

If smooth-yellow, *SY*, and wrinkled-green, *WG*, are crossed, all the offspring are smooth-yellow, but they carry concealed the recessive determiners for wrinkledness and greenness according to the formula *S*(*W*)*Y*(*G*). When the determiners of these cross-breds segregate out during the maturation of the germ-cells, they may recombine so as to form four possible double gametes, namely, smooth-yellow, *SY*, and wrinkled-green, *WG*, which are exactly like the grand-parental determiners from which they arose, and in addition, two entirely new combinations, smooth-green, *SG*, and wrinkled-yellow, *WY*.

Since the male and the female cross-breds are each furnished with these four possible gametic combinations, the possible number of zygotes formed by their union will be sixteen ($4 \times 4 = 16$). That is, the monohybrid proportion of 3 to 1 in dihybrid combinations is squared, $(3+1)^2=16$.

It of course does not follow that the offspring in dihybrid crosses will always be sixteen in number, or that they will always conform strictly to the theoretical expectation of $(3+1)^2$. The offspring obtained undoubtedly obey the laws of chance, but the greater

the number of offspring, the nearer they come to falling into the expected grouping.

The sixteen possible zygotes resulting from a dihybrid cross will give rise to sixteen possible kinds of individuals which in turn, as will be demonstrated directly, present four kinds of phenotypic and nine kinds of genotypic constitutions.

A dihybrid mating, using the same symbols employed in the case just described, would be expressed algebraically as follows:—

```
SG+    WY+    SY+    WG = all the possible egg gametes
SG+    WY+    SY+    WG = all the possible sperm gametes
SGSG+ SGWY+ SGSY+ SGWG
      SGWY               +WYWY+ WYSY+ WYWG
             SGSY              + WYSY        +SYSY+ SYWG
                    SGWG             + WYWG        + SYWG+WGWG
SGSG+2SGWY+2SGSY+2SGWG+WYWY+2WYSY+2WYWG+SYSY+2SYWG+WGWG
```

The second and the ninth items in this result are alike; by combining them the revised result reads:—

SGSG+4SGWY+2SGSY+2SGWG+WYWY+2WYSY+2WYWG+SYSY+WGWG

There are then these nine different combinations of germinal characters or nine different genotypes in any dihybrid cross. By placing the recessive characters in parentheses whenever the corresponding dominant is present, to indicate that the dominant causes the former to recede from view, these nine genotypes may be combined into four phenotypes as shown in the table at the top of page 110.

From this analysis it may be said that the Mendelian ratio for a typical dihybrid is phenotypically 9:3:3:1, while that for a monohybrid, as we have

Phenotypes	9 *SY*	3 *SG*	3 *WY*	1 *WG*
Genotypes	4 *S(G)(W)Y* 2 *S(G)SY* 2 *SY(W)Y* *SYSY*	*SGSG* 2 *SG(W)G*	*WYWY* 2 *WYW(G)*	*WGWG*

already seen, is phenotypically 3 : 1. This expected ratio corresponds essentially with the actual results

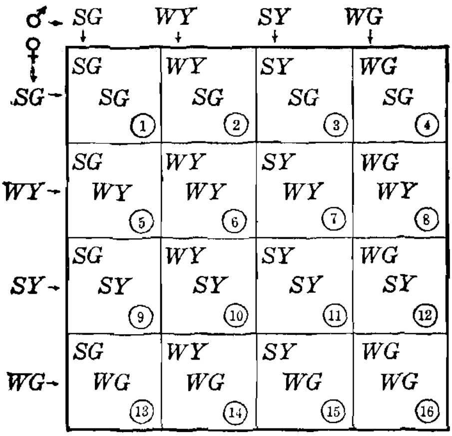


Fig. 18.—Diagram to illustrate the possible combinations arising in the second filial generation (F_2) following a cross between yellow-smooth, YS, and green-wrinkled, GW, peas.

which Mendel obtained in crossing smooth-yellow and wrinkled-green peas.

Figure 18 presents a graphic representation of the different combinations resulting from a dihybrid cross following the checkerboard plan used in Figure 16 to illustrate monohybrids.

The nine genotypes and four phenotypes which

Phenotypes	9 *SY*	3 *SG*	3 *WY*	1 *WG*
Genotypes	4 *S*(*G*)(*W*)*Y* 2 *S*(*G*)*SY* 2 *SY*(*W*)*Y* *SYSY*	*SGSG* 2 *SG*(*W*)*G*	*WYWY* 2 *WYW*(*G*)	*WGWG*

already seen, is phenotypically 3 : 1. This expected ratio corresponds essentially with the actual results

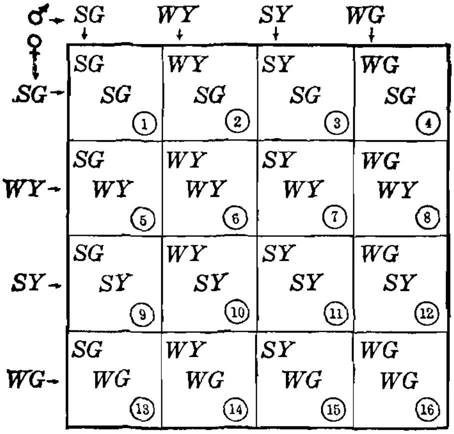


Fig. 18.—Diagram to illustrate the possible combinations arising in the second filial generation (F_2) following a cross between yellow-smooth, YS, and green-wrinkled, GW, peas.

which Mendel obtained in crossing smooth-yellow and wrinkled-green peas.

Figure 18 presents a graphic representation of the different combinations resulting from a dihybrid cross following the checkerboard plan used in Figure 16 to illustrate monohybrids.

The nine genotypes and four phenotypes which

result from a dihybrid cross are shown in the following table:

Number in Each Class	Genotype	Number of Squares in Fig. 18	Phenotype	Number in Each Class
1	*SYSY*	11	*SY*	9
2	*(W)YSY*	7 · 10		
2	*S(G)SY*	3 · 9		
4	*S(G)(W)Y*	2 · 5 · 12 · 15		
1	*SGSG*	1	*SG*	3
2	*SG(W)G*	13 · 4		
1	*WYWY*	6	*WY*	3
2	*WYW(G)*	8 · 14		
1	*WGWG*	16	*WG*	1
16				16

Another illustration of dihybridism is shown in Figures 19 and 20 based upon data furnished by the Davenports.[1] In the matings given here, dark or pigmented hair, represented by the solid black circles, is dominant over light-colored, that is, unpigmented or slightly pigmented hair, symbolized by the open circles, while curly hair is dominant over straight, represented by crooked and straight lines respectively in the diagram. In other words, the presence of pigment is dominant over the absence of pigment, while the factor that causes curliness is dominant over the absence of this factor, with respect to human hair.

[1] "Heredity of Eye-color in Man," *Science*, N. S. 26, p. 589, 1907; "Heredity of Hair Form in Man," *Amer. Nat.* 42, p. 341, 1908. Davenport, C. B. and G. C.

When a homozygous individual with dark curly hair crosses with a homozygous individual with light

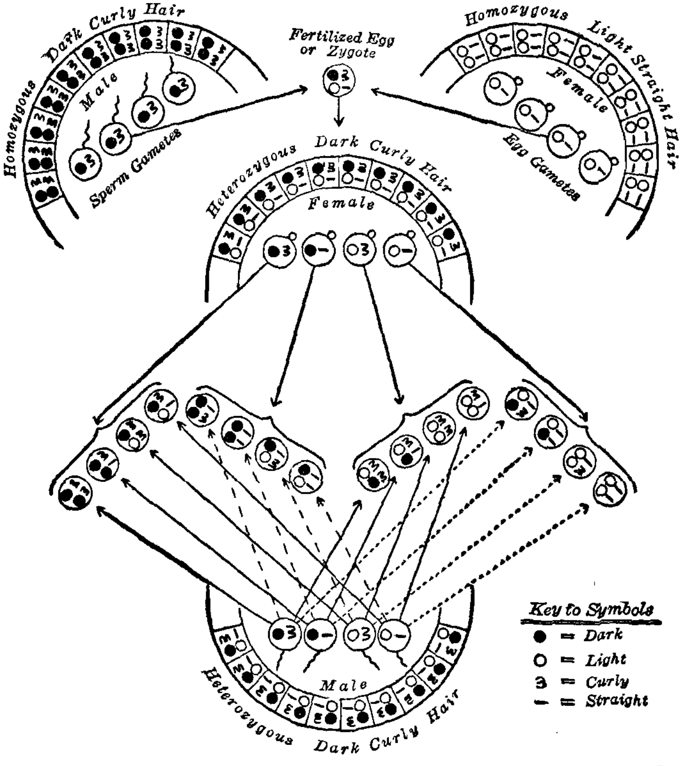
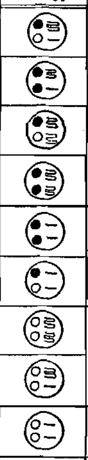


FIG. 19.—The heredity of human hair according to data by C. B. and G. C. Davenport. The arcs represent the somatoplasms of four individuals. Within the arcs are the gametes formed by these individuals. The dominant character is placed on the outside of the arc where it will be visible.

straight hair, all the offspring have dark curly hair. The dark curly-haired individuals of this second generation, however, are heterozygous with respect to

each of these two hair characters. When any two individuals having this particular genotypic composition mate, therefore, they may produce any one of four possible phenotypes—dark curly, dark straight, light curly or light straight haired individuals. These four phenotypes in turn will present nine different genotypic combinations out of sixteen possible cases, as shown in Figure 20.



Number in each class	Genotype	Phenotype	Number in each class
4		*Dark curly*	9
2			
2			
1			
1		*Dark straight*	3
2			
1		*Light curly*	3
2			
1		*Light straight*	1
16			16

FIG. 20.—Diagrams showing the possible genotypic and phenotypic combinations resulting when two heterozygous individuals with dark curly hair mate. Symbols are the same as in Figure 19.

Figure 19 furthermore serves to make clear, *first*, the distinction between somatoplasm and germplasm; *second*, the maturation of germ-cells; *third*, the segregation of gametes; and *fourth*, the formation of zygotes in sexual reproduction.

The cells of the somatoplasm are represented as making up the arcs within which are inclosed the germ-cells after their reduction through maturation, which results in giving to each germ-cell half the number of determiners that are present in the somatic cells.

It will be remembered that when two gametes, or

mature germ-cells, unite, they form a zygote having the proper number of determiners normal to the species in question instead of double that number. Symbols for dominant characters in the diagram are placed on the *outside* of the somatic arcs, because these are the characters that are visible or phenotypic, while the non-apparent recessives are placed on the inside out of sight.

11. The Case of the Trihybrid

Mendel went even further and computed the possibilities which would result when two parents were crossed differing from each other with respect to three unit characters. He found that the results actually obtained by breeding closely approximated the theoretical expectation.

This expectation in the case of a trihybrid cross is that the cross-breds resulting will all exhibit the three dominant characters, while their genotypic constitution will include six factors, namely, these three dominant characters plus their corresponding recessives or "absences."

Cross-breds of the first generation will, therefore, have eight possible kinds of triple gametes and when interbred may form a possible range of sixty-four (8×8) different zygotes, which corresponds to a monohybrid raised to the third power $(3+1)^3$. These sixty-four zygotes group together in eight different phenotypes and twenty-seven different genotypes as shown on page 116.

The trihybrid cross with its resulting combinations

is well illustrated by Castle's work on guinea-pigs which confirms the Mendelian hypothesis on an extensive scale. In Figure 21 dominant characters are repre-

♂→ ♀↓	*RSP* ↓	*RsP* ↓	*RSp* ↓	*Rsp* ↓	*rSP* ↓	*rsP* ↓	*rSp* ↓	*rsp* ↓
RSP→	*RSP* *RSP*	*RsP* *RSP*	*RSp* *RSP*	*Rsp* *RSP*	*rSP* *RSP*	*rsP* *RSP*	*rSp* *RSP*	*rsp* *RSP*
RsP→	*RSP* *RsP*	*RsP* *RsP*	*RSp* *RsP*	*Rsp* *RsP*	*rSP* *RsP*	*rsP* *RsP*	*rSp* *RsP*	*rsp* *RsP*
RSp→	*RSP* *RSp*	*RsP* *RSp*	*RSp* *RSp*	*Rsp* *RSp*	*rSP* *RSp*	*rsP* *RSp*	*rSp* *RSp*	*rsp* *RSp*
Rsp→	*RSP* *Rsp*	*RsP* *Rsp*	*RSp* *Rsp*	*Rsp* *Rsp*	*rSP* *Rsp*	*rsP* *Rsp*	*rSp* *Rsp*	*rsp* *Rsp*
rSP→	*RSP* *rSP*	*RsP* *rSP*	*RSp* *rSP*	*Rsp* *rSP*	*rSP* *rSP*	*rsP* *rSP*	*rSp* *rSP*	*rsp* *rSP*
rsP→	*RSP* *rsP*	*RsP* *rsP*	*RSp* *rsP*	*Rsp* *rsP*	*rSP* *rsP*	*rsP* *rsP*	*rSp* *rsP*	*rsp* *rsP*
rSp→	*RSP* *rSp*	*RsP* *rSp*	*RSp* *rSp*	*Rsp* *rSp*	*rSP* *rSp*	*rsP* *rSp*	*rSp* *rSp*	*rsp* *rSp*
rsp→	*RSP* *rsp*	*RsP* *rsp*	*RSp* *rsp*	*Rsp* *rsp*	*rSP* *rsp*	*rsP* *rsp*	*rSp* *rsp*	*rsp* *rsp*

FIG. 21.—Diagram showing the possible combinations in a guinea-pig trihybrid of the F_2 generation. *R*, rosetted coat; *r*, non-rosetted coat (absence of *R*); *S*, short hair; *s*, angora hair (absence of *S*); *P*, pigmented; *p*, albino (absence of pigment). The eight possible triple gametes of each parent are placed in the upper and left hand margins respectively. Each of the sixty-four squares represents a possible zygote or fertilized egg, having received a triple gamete from each parent.

sented by capital letters, while recessives or absences are indicated by corresponding small letters.

When a smooth, or non-rosetted (*r*), short-haired (*S*), pigmented (*P*) guinea-pig is crossed with a

Number in each class	Genotype	Phenotype	Number in each class
1	*SS PP RR*	*SPR* Short, pigmented, rosetted	27
2	*SS Pp RR*		
2	*Ss PP RR*		
4	*Ss Pp RR*		
2	*SS PP Rr*		
4	*SS Pp Rr*		
4	*Ss PP Rr*		
8	*Ss Pp Rr*		
1	*SS pp RR*	*SpR* Short, albino, rosetted	9
2	*Ss pp RR*		
2	*SS pp Rr*		
4	*Ss pp Rr*		
1	*ss PP RR*	*sPR* Angora, pigmented, rosetted	9
2	*ss Pp RR*		
2	*ss PP Rr*		
4	*ss Pp Rr*		
1	*SS PP rr*	*SPr* Short, pigmented, non-rosetted	9
2	*SS Pp rr*		
2	*Ss PP rr*		
4	*Ss Pp rr*		
1	*ss pp RR*	*spR* Angora, albino, rosetted	3
2	*ss pp Rr*		
1	*SS pp rr*	*Spr* Short, albino, non-rosetted	3
2	*Ss pp rr*		
1	*ss PP rr*	*sPr* Angora, pigmented, non-rosetted	3
2	*ss Pp rr*		
1	*ss pp rr*	*spr* Angora, albino, non-rosetted	1
64			64

rosetted (*R*), long-haired (*s*), albino (*p*) guinea-pig, all the offspring appear to be of one phenotypic constitution, namely, rosetted, short-haired, and pigmented (*RSP*). Their genotypic constitution is represented by the formula *RrSsPp*. These six factors may form eight possible triple gametes, as follows: *RSP*, *RsP*, *RSp*, *Rsp*, *rSP*, *rSp*, *rsP*, *rsp*. When two germ-cells each made up of these eight triple gametes unite in sexual reproduction, they will give rise to sixty-four (8×8) possible zygotes as displayed in Figure 21.

An analysis of Figure 21 shows among the offspring eight different phenotypes in the ratio of 27:9:9:9:3:3:3:1 and 27 different genotypes in the proportions indicated on page 116. The *order* of the three pairs of symbols is changed from that in Figure 21 to emphasize the fact that with independent unit characters the order is immaterial.

Sketches, drawn from photographs in Castle's "Genetics and Eugenics," of the eight phenotypically different guinea-pigs here described are shown in Figure 22.

12. Summary

Three principles are concerned in Mendel's law: independent unit characters, dominance, and segregation.

a. Independent Unit Characters. An organism, although acting together as a physiological and morphological whole, may be regarded from the point of view of heredity as consisting of a large number of independent heritable unit characters.

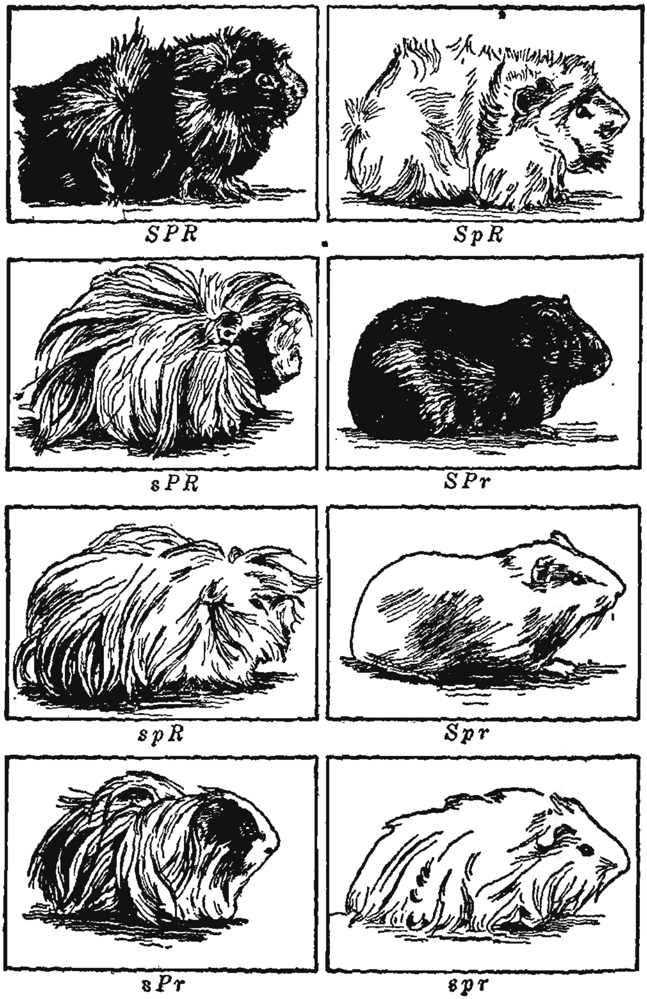


Fig. 22.—The eight phenotypically different kinds of guinea-pigs in the F_2 generation of a trihybrid. S = short hair; s = long hair or angora; P = pigmented coat; p = non-pigmented coat or albino; R = rough or rosetted coat; r = smooth coat. Drawn from Castle's photographs by C. J. Fish.

b. Dominance. In every individual there are two determiners for every unit character, one derived from each parent. If this pair is different, *i. e.*, if the zygote is a heterozygote, one dominates the other and determines the apparent character of the organism.

The alternative *recessive* characters, although they may be present in the germplasm, are unable to become manifest in the somatoplasm so long as the dominant characters are present. When, however, the dominant determiner is absent, and the recessive is duplicated, the recessive character becomes manifest.

c. Segregation. The determiners of unit characters, although they may be intimately associated together in the individual, during the complicated process of maturation that always precedes the formation of a new individual, separate or segregate out as if independent of each other and thus are enabled to unite into new combinations.

13. The Practical Application

Although the ratios for more than a trihybrid were computed by Mendel, the experimental test was not carried out by him, since it involves such large and complicated proportions.

In the case of four differing unit characters in the parental generation, the offspring of the quadruple hybrids derived from such an ancestry would include 256 or $(3+1)^4$ possibilities instead of 64 or $(3+1)^3$, as in the case of trihybrids. When ten differing characters are combined in the parental generation,

there would result over a million possible kinds of offspring among the hybrids of the second filial generation, $(3+1)^{10}=1,048,576$.

From the foregoing it is apparent that in practical breeding the only hope lies in dealing with not more than one or two characters at a time. Since unit characters usually behave independently of each other, one may breed *for a single character* until it is segregated out in a homozygous, that is pure, condition, and then in the same way obtain a second character, a third, and so on.

This is not difficult if the character sought is a recessive for, in that case it is already homozygous or pure and consequently appears. When a character is dominant it takes longer to determine whether the individual is heterozygous (hybrid) or homozygous (pure).

14. Conclusion

The Mendelian method is an attempt to analyze the behavior of a particular characteristic in heredity rather than to get at the lump performance of the individual as a whole. Herein lies the scientific control of heredity which the trinity of Mendelian principles namely, independent unit characters, segregation, and dominance, has placed in human hands. Following this method there can be obtained in a few generations of properly directed crosses, combinations of characters united in one strain that formerly were never obtained at all or were only hit upon by the merest chance at long intervals.

CHAPTER VI

THE PURE LINE AND SELECTION

1. Galton's Law of Regression

Galton was one of the first [1] to attempt to express mathematically the relationship between parents and offspring by means of treating statistically a single unit character. According to Galton, a mathematical expression of the relationship between two generations should serve as a corner-stone of heredity.

What Galton did was to take human stature as a unit character in comparing 204 English parents and their 928 adult offspring, because human stature is not complicated by environmental influences and is consequently, a purely hereditary matter.

The results of his measurements expressed in inches are shown in Figure 23 in which the circles connected by the diagonal line represent the graded parental heights, while the arrowpoints indicate the average heights of the offspring in each group.

This illustrates Galton's *Law of Regression* or the tendency in successive generations toward mediocrity. The law may be stated as follows:—

Average parents tend to produce average children; minus parents tend to produce minus children; plus

[1] "Hereditary Genius," 1869.

parents tend to produce plus children; *but the progeny of extreme parents, whether plus or minus, inherit the parental peculiarities in a less marked degree than the latter were manifested in the parents themselves.*

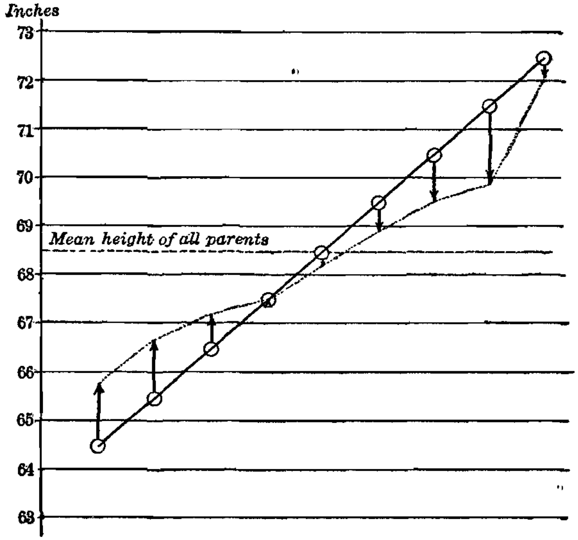


Fig. 23.—Scheme to illustrate *Galton's law of regression.* The circles represent graded groups of parental height while the arrowpoints indicate the average heights attained by the respective offspring. The offspring of undersized parents are taller, and of oversized parents are shorter than their respective parents. Based on data from Galton.

2. The Idea of the Pure Line

It was Galton's law of regression that suggested to the Danish botanist Johannsen a possible means of controlling heredity. In his mind arose the question whether it would not be possible by continually breeding

from plus parents, granting that plus parents produce plus offspring and making allowance for some regression to type, to shove over the offspring more and more into the plus territory and so to establish a plus race.

To test this hypothesis, Johannsen selected beans, *Phaseolus*, with which to experiment, since this group of plants is self-fertilizing, prolific, and easily measurable. Somewhat to his surprise, the beans refused to shove over as much as expected. That is, big beans did not yield principally big offspring, nor little beans little offspring, according to the expectation, although they each produced offspring that varied in the manner of fluctuating variability around an average unlike the parental type. This gave Johannsen the idea that he was using mixed material, so he next isolated the progeny of single beans, which, being self-fertilized for many generations, each constituted unmistakably a single hereditary line. In this way nineteen beans, now famous, became the known ancestors of Johannsen's original nineteen "pure lines," a further study of which has led the way to some of the most brilliant biological discoveries of recent years.

A pure line has been defined by Johannsen as "the descendants from a single homozygous organism exclusively propagating by self-fertilization," and more briefly by Jennings as "all the progeny of a single self-fertilized individual."

It should be pointed out, however, that this technical idea of a "pure line" is not at all the same as that which the breeder has in mind when he uses the same term. The nearer individuals can be bred to conform to an

arbitrary standard agreed upon, the better they illustrate the stock-breeder's idea of a pure line. For example, in "The Standard of Perfection," a book published by the American Poultry Association, there are recognized 42 breeds and 121 varieties of chickens. To belong to any particular breed in this gallinaceous Blue Book the chicken must *look the part* regardless of its germinal derivation.

To the biologist, on the contrary, the pure line is like an imaginary mathematical concept depending entirely upon similarity of the determining hereditary complex. The biologist's pure line is genotypic. The stock-breeder's is phenotypic, a difference of definition which has given rise to considerable confusion.

In a certain general way it will be seen that the pure line stands over against mutation, since it is concerned with the conservative maintenance of type while mutation attempts to change it.

The inevitable monotony of a pure line may be considerably masked by individual somatic modification. DeVries has said paradoxically, "The pure line is completely constant and extremely variable." That is, it is "completely constant" except for mutations, and it is "extremely variable" in the somatic development that may be attained by separate individuals.

3. Johannsen's Nineteen Beans

To return to experiments with beans, Johannsen found out that the progeny of every one of his pure lines varied around its own mean, which was different

in each of the nineteen instances. When, however, extremes from any pure line series were selected and bred from, the results showed *complete regression* away from the extreme condition of the parent bean back to the

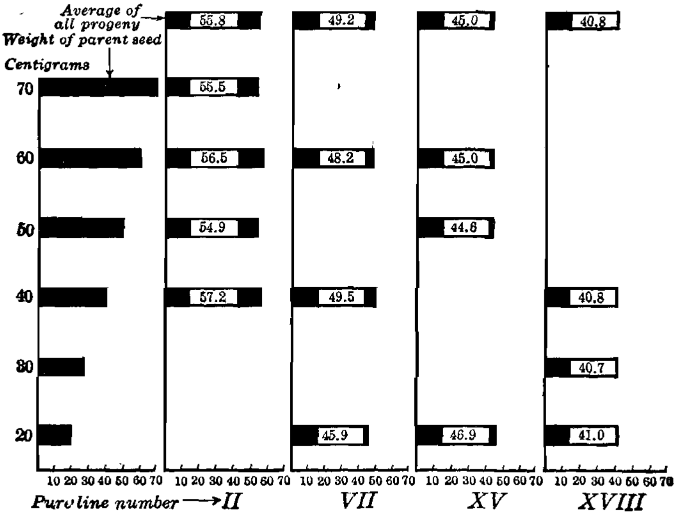


Fig. 24.—The result of selection in four pure lines of beans. The vertical columns, representing the average progeny from different sized parents all derived from the same pure line, contain groups nearer alike than the horizontal columns, representing progeny from the same sized parents, but different pure lines. All the numbers indicate centigrams. Data from Johannsen.

type of the entire pure line in question. That is, *selection within a pure line is absolutely without effect* in modifying a particular character in the offspring of the line in question.

This is illustrated in Figure 24 in which the results of selecting for size in the year 1902 is shown for four

pure lines only. The average for each pure line is given at the top of its column. When, for example, beans weighing 60 cg. were selected from pure lines II, VII, and XV, the average weights of their progeny were 56.5, 48.2, and 45.0 cg. respectively, which in each instance is nearer to the average for the pure line than to the weight of the parental seed.

It will be seen at once that the averages in the vertical columns are nearer alike than the averages in the horizontal columns. In other words, the beans bred true to their pure line rather than to their fluctuating parent.

As a further example of this law, take the result of selection for six years in pure line I as shown in the accompanying table and in Figure 25.

Harvest Year	Mean Weight of Selected Parent Seed		Mean Weight of Offspring	
	Minus	Plus	From Minus Parent	From Plus Parent
1902	60	70	63.15	64.85
1903	55	80	75.19	70.88
1904	50	87	54.59	56.68
1905	43	73	63.55	63.64
1906	46	84	74.38	73.00
1907	56	81	69.07	67.66

It is evident, for instance, that in 1907 the smallest beans, weighing an average of 56 cg., gave an average progeny weighing 69.07 cg., while the largest ones for the same year, weighing an average of 81 cg., produced nearly the same average in their progeny as did the smallest beans, that is, 67.66 cg.

Incidentally all the progeny from both large and small parents averaged notably less in 1904 than all the progeny from large and small parents in 1906, a result due to a "poor year" when certain factors of environment were unfavorable. Such unfavorable conditions, however, are known to influence in no way the hereditary qualities of the beans. Thus it appears that, although the progeny of a pure line present plenty of variations of the fluctuating type, due probably to environmental differences in nutrition, moisture, etc., such variations are quite ineffectual so far as inheritance is concerned, and it makes no difference whether the largest or the smallest beans within a pure line are selected from which to breed, the result will be the same, in that there is a complete return to mediocrity or type with no "inheritance" of the parental modification. As a matter of fact in 1903, 1906 and 1907 the lighter parents gave heavier progeny than the heavier parents.

It will be seen at once that here is a discovery of far-reaching importance which may require us to reconstruct certain cherished ideas about the part played in the evolution of species, as well as in heredity, by natural selection.

4. The Distinction between a Population and a Pure Line

A mixture of pure lines has been called a *population* (Johannsen).

It is not possible to distinguish by inspection a group

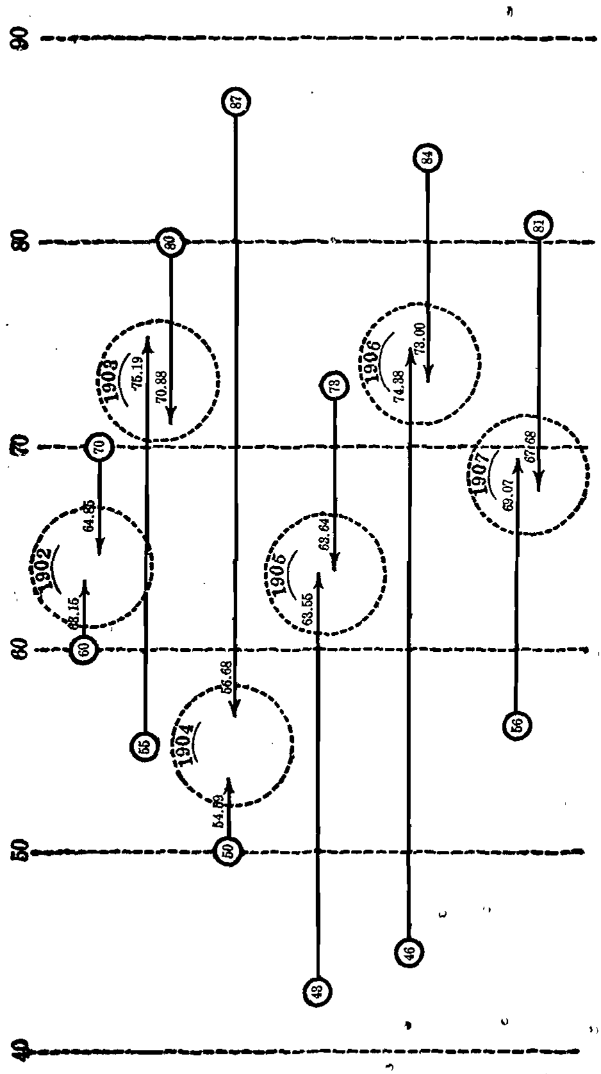


FIG. 25.—Diagram showing the negative result of selection for six years within "pure line 1" of Johannsen's beans. The small circles indicate the selected parents and the arrowpoints their respective progeny. In every case the weight of the average offspring is nearer the mean for the pure line than it is to that of its respective parent. Data from Johannsen.

of individuals composing a pure line from a group making up a population, since both may be phenotypically alike. Fluctuations about the average occur in both cases with no appreciable difference in character, although such fluctuations, when they occur within a pure line, are simply somatic differences caused in general probably by modifications in nutrition or some other external factor of environment, while fluctuations in a population include not only modifications of this transient nature, but also permanent hereditary differences due to germinal differences in the various pure lines of which the population is composed.

Johannsen has made the distinction between pure lines and populations clear by the following figure (Fig. 26), in which five pure lines of beans are combined artificially to form a population.

The beans which make up the pure lines noted in this figure are represented inclosed within inverted test tubes. The beans in any single tube are all of one size. Tubes vertically superimposed upon each other also contain only beans of one size.

Thus it is seen that what may be a rare size of bean in one line, for instance that in the left-hand tube of *pure line 3*, may be identical with the commonest size in another line, as *pure line 2*. The five pure lines represented in Figure 26 are combined in a *population* at the bottom of the figure. In this population array the five pure lines are hidden.

Hence, while selection within a pure line has no hereditary influence, it is evident that selection within a population may shift or move over the type of the

progeny obtained, in the direction of the selection simply by isolating out a pure line of one type. Thus beans chosen from the extreme left-hand test tube in the population cited would belong only to *pure line 2*, while those taken from the extreme right-hand test tube could belong only to *pure line 3.*

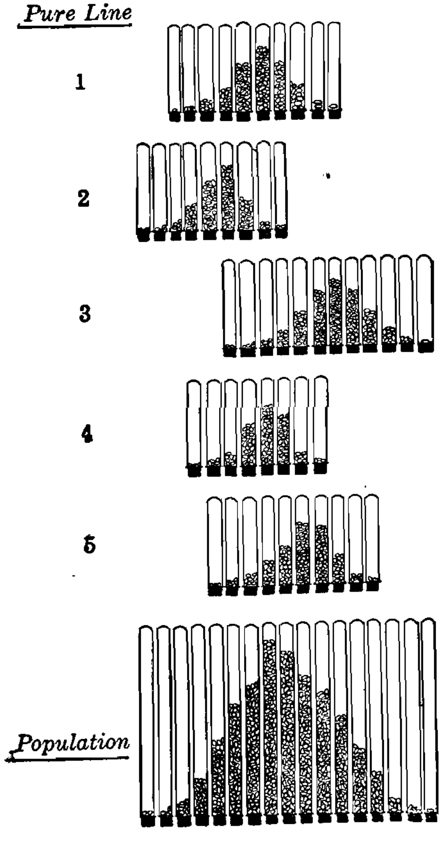


FIG. 26.—Diagrams showing five *pure lines* and a *population* formed by their union. The beans of each pure line are represented as assorted into inverted test tubes making a curve of fluctuating variability. Test tubes containing beans of the same weight are placed in the same vertical row. After Johannsen.

Galton's "law of regression," namely, that minus parents give minus offspring and plus parents plus offspring, with a tendency to reversion from generation to generation, depends simply upon a partial but not complete isolation of pure lines out of a population.

From this distinction between pure lines and populations it is clear why breeders in selecting for a particular character out of their stock need to keep on selecting continually in order to maintain a certain standard. As soon as they cease this vigilance, there is a "reversion to type" or, as they say, "the strain runs out," which means that the pure lines become lost in the mixed population which inevitably results as soon as selective isolation of the pure line ceases.

Such reversion must always be the case in dealing with a population made up of a mixture of pure lines, for only by the isolation of pure lines can the constancy of a character be maintained. When, however, a pure line is once isolated, then all the members of it, large as well as small, are equally efficient in maintaining the pure line in question, regardless of their phenotypical constitutions.

Conceding that natural history and common usage as well as the older theories of heredity are concerned with phenotypic constitution of organisms, we are now coming to see more clearly than before that heredity must always be a case of *similarity in origin*, that is, in germinal composition, and that similarity in appearance by no means always indicates similarity in origin or true relationship.

The assumption that similarity in appearance does indicate relationship has been made the foundation of many conclusions in comparative anatomy and phylogeny, but to the modern student of genetics who places his faith in *things as they are, rather* than in *things as they seem to be*, conclusions based upon phenotypical

distinctions alone have in them a large source of error which must be taken into account.

In a museum of heredity, should such a collection ever be assembled, the specimens would not be arranged phenotypically as they are in an ordinary museum where things that look alike are placed together as if in bonds of relationship, but they would be arranged *historically* from a genetic point of view to show their true origin one from another.

5. Cases Similar to Johannsen's Pure Lines

Although, according to Johannsen, pure lines are "the progeny of a single self-fertilized individual," it is plain that in at least three other possible cases something quite similar to "pure lines" may be obtained.

These are *clones*, *parthenogenetic progeny* and *homozygous crosses*. "In principle pure lines, parthenogenetic reproduction and vegetative propagation are concerned with nearly the same situation" (Morgan).

First, in asexual reproduction where the progeny are simply the result of continued fission of the original individual, a pure line may be said to continue from generation to generation because it is a germinally unchanged sequence of individuals. Such an asexual progeny is termed a *clone* (Webber). Shull's definition of a clone is "a group of individuals of like genotypic constitution, traceable through asexual reproductions to a single ancestral zygote, or else perpetually asexual."

Second, in cases of *parthenogenesis*, the progeny

arising from a single female individual without the customary maturation of the germ-cells which accompanies sexual reproduction, constitute a pure line or an unmixed strain because as in clones there has been no segregation nor addition of outside germplasm.

Third, in *homozygous crosses* when two organisms identical in their germinal determiners inbreed, their progeny will form a pure line just as truly as two parents that are united in a single hermaphroditic individual produce a pure line progeny as the result of self-fertilization.

In the case of clones and parthenogenesis it should be pointed out that the "pure line" is assured only so long as asexual reproduction continues. It is quite possible for an organism, even heterozygotic in composition, to continue to breed true or to produce an apparently pure line so long as asexual methods are employed. As soon as such an organism, however, changes to the sexual method of reproduction, segregation of characters may occur and different combinations result. A pure line, therefore, implies *freedom from admixture of different germplasm* rather than any necessary equality or likeness of individuals.

The different kinds of "pure lines" are diagrammatically represented in Figure 27.

6. Selection within a Pure Line

The basic idea of the pure line concept is that every member of any pure line is genetically identical with every other member of the same fraternity, therefore,

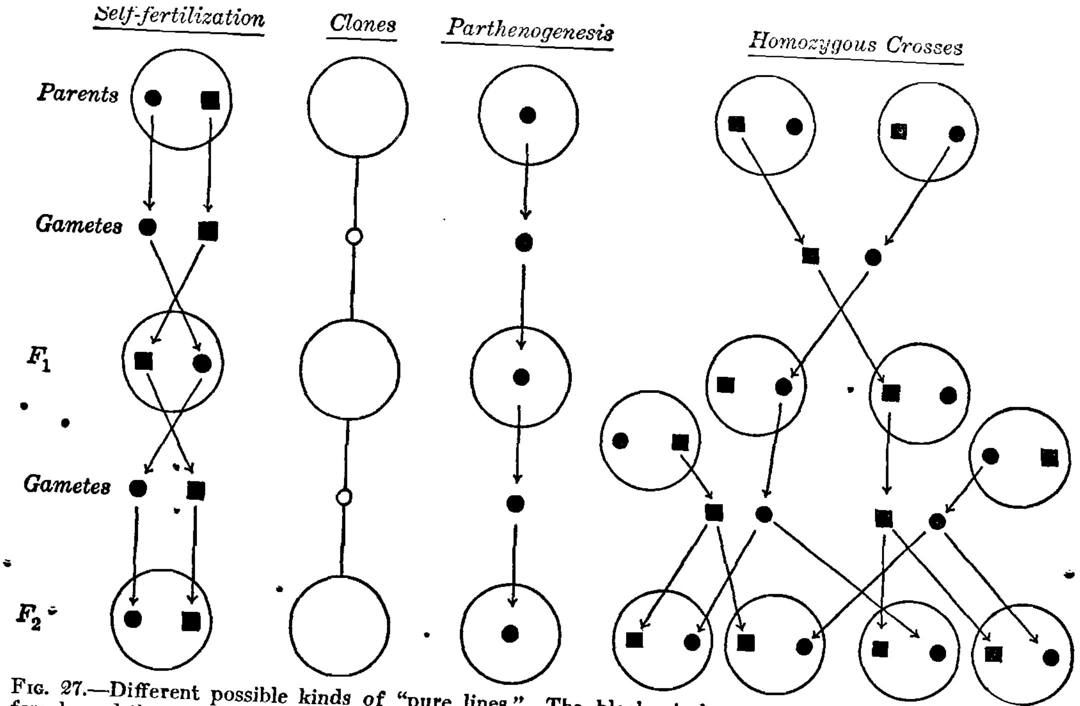


Fig. 27.—Different possible kinds of "pure lines." The black circles represent germplasm from the female and the squares the *same kind* of germplasm from the male.

any differences found between individuals of a pure line are entirely somatic and not hereditary.

The importance of the problem of pure line selection for any general consideration of the mechanism of evolution is at once apparent. There have been many recent investigations besides those of Johannsen to test the result of selection within the four kinds of "pure lines." Some of these investigations are enumerated in the table on pages 136 and 137.

A. VILMORIN'S WHEAT

It is apparent in the first section of the following table that the pure line *sensu stricto*, that is, the pure line of Johannsen, must be studied with plants alone, since among animals only certain highly specialized parasitic worms, which do not lend themselves readily to selection experiments, produce offspring by means of self-fertilization. The work of the other authors upon plants, mentioned in the first group of the table, is in entire agreement with the work of Johannsen.

The noteworthy contribution of L. de Vilmorin consists in a detailed comparison of preserved specimens of certain pure lines of wheat which were isolated in France about 1840, with their lineal descendants of to-day. In spite of continuous selection for betterment within these self-fertilized strains during more than 60 years, their constancy has been maintained.

B. CLONES

With respect to selection within a clone there is an apparent conflict of results.

THE RESULTS OF SELECTION WITHIN A PURE LINE

Kind of pure line	Author	Organism	Character selected	Result
Progeny of a single self-fertilized individual	Johannsen, '03	Beans	Size	No effect
	"	Barley	Mealiness of kernel	" "
	Nilsson	Wheat Oats Barley	Various characters	" "
	Surface and Pearl	Oats	Yield per acre	" "
	Fruwirth, '17	Lentils Peas Soy beans Lupines		" "
	L. de Vilmorin	Wheat		" "
Clones	Wolf, '09	Bacteria	Pigment production	" "
	Barber, '07	"		" "
	Winslow and Walker, '09	"		" "
	Meader, '19	"	Form, fermentative reaction, virulence	" "
	East, '09-'10	Potato		" "
	Vogler, '14	Garlic		" "
	Stout, '15	Coleus	Color pattern	Effective
	Mendiola, '19	Lemna	Size and shape of frond, speed of budding	No effect
	Jennings, '08	Paramecium	Size	" "
	" '16	Difflugia	Six shell characters	Effective
	Calkins and Gregory, '13	Paramecium	Size, rate of fission, etc.	"
	Jollos, '13	"	Resistance to arsenical poisoning	No effect
	Stocking, '15	"	Abnormalities	Effective in some lines
	Middleton, '15	Stylonychia	Fission-rate	Diverse strains from one

THE RESULTS OF SELECTION WITHIN A PURE LINE—*Continued*

Kind of Pure line	Author	Organism	Character selected	Result
	Ackert, '16	Paramecium	Size	No effect
	Root, '18	Centropyxis	Shell characters, fission-rate	Effective
	Hegner, '19	Arcella	Shell characters	Diverse strains from one
	Hanel, '08	Hydra	No. of tentacles	No effect
	Lashley, '16	"	" " "	" "
Parthenogenetic progeny	Woltereck, '09	Hyalodaphnia	Length and shape of "head"	Temporary temperature effect
	Agar, '13	Simocephalus		No effect
	" '14	Aphids		" "
	Ewing, '14	"	Length of honeydew tubes, antennæ and body	" "
	Kelly, '13	"	Length of antennal joints	" "
	Banta	Daphnids	Light reactions	Effective in one line
	" '19	Simocephalus	Sex intergrades	"Somewhat effective"
Homozygous Crosses	Smith	Maize	Oil and protein content	Effective
	Tower, '06	Potato beetle	Pigmentation	No effect
	May, '17	Drosophila	Bar-eye	" "
	Zeleny, '20	"	"	Ineffective after 3 to 5 generations
	McDowell, '15	"	Thoracic bristles	Effective
	Reeves, '16	"	Thoracic bristles	"
	Payne, '20	"	Thoracic bristles	Effective for several generations
	Sturtevant, '18	"	Dichaet bristles	Effective
	Pearl	Hen	Fecundity	No effect
	Castle and Phillips	Hooded rat	Coat pattern	Effective

In bacteria it is possible to isolate out variants from a single strain but in none of the cases is the origin of the supposed "clone" unquestionably *from a single bacterium* as it would need to be in order to form a pure line, so that what has occurred in all probability is the simple assortment of a pure line from a population.

Among the protozoa, which reproduce asexually by fission, much painstaking experiment and observation

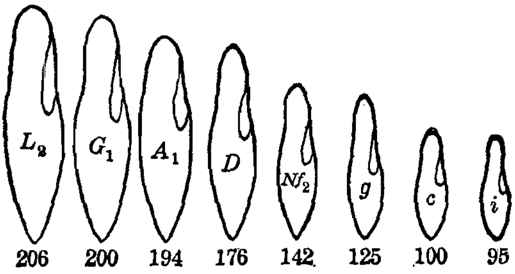


FIG. 28.—Eight pure races of *Paramecium*. The actual mean length of each race is given in micra below the corresponding outline. Magnified about 230 diameters. After Jennings.

has been made, notably by Jennings and various investigators whom he has inspired.

For example, Jennings found that Paramecia differ from each other in size, structure, physical character, and rate of multiplication as well as in the environmental conditions required for their existence and, furthermore, that these differences, in an hereditary sense, are "as rigid as iron."

With respect to the character of mean length he

was able to isolate eight races, or pure lines, whose average size, drawn to scale, is shown in Figure 28.

Each of these pure lines produced a progeny which exhibited a considerable range of fluctuating variation. The offspring of *pure line D*, for example, varied from 256 to 80 micra[1] in length with an average of 176 micra, as shown in Figure 29, where samples of the different classes of variants in *pure line D* are arranged in a series.

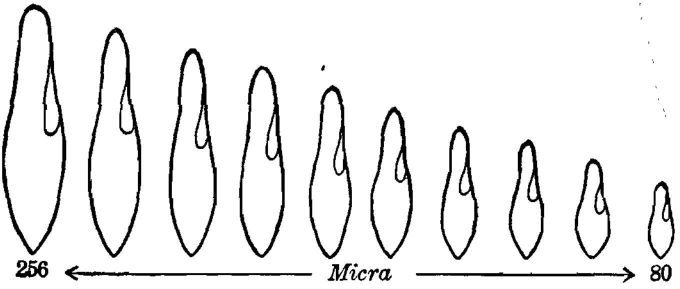


FIG. 29.—Diagram of a single race (*D*) showing the variation in the size of the individuals. Magnified about 230 diameters. After Jennings.

A single representative of each of the different classes of variants out of all the eight pure lines bred by Jennings is shown in Figure 30.

Each horizontal row represents a single race or pure line, the average size of which is indicated by the sign +. The mean length of the entire lot, as shown by the vertical line, is 155 micra. The total number of individuals belonging to each size is not indicated, but

[1] A micron is 1-1000th of a millimeter.

in every horizontal line their number is more numerous near the average for that line and less numerous at

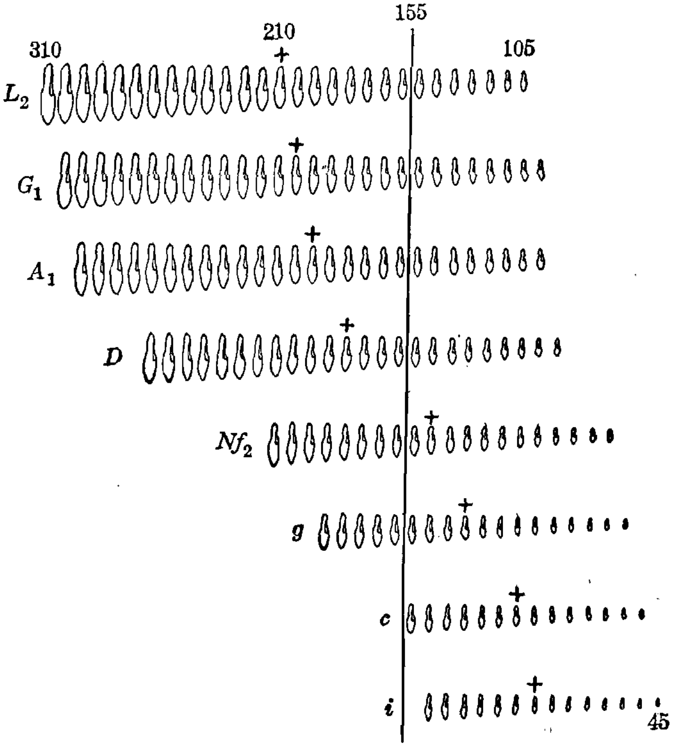


FIG. 30.—Diagram of the species *Paramecium* as made up of the eight different races shown in Figure 28. Each horizontal row represents a single race. The individual showing the mean size in each race is indicated by a cross placed above it. The mean for the entire lot is at the vertical line. The magnification is about 24 diameters. After Jennings.

the extremes, thus forming the typical normal frequency curves of fluctuating variability.

The significant fact about these series is that ex-

treme individuals selected from any pure line do not reproduce extreme sizes like themselves, but instead, a progeny varying according to the laws of chance around the average standard of the particular line from which it came. Thus quite independently of Johannsen, Jennings arrived at the same general conclusion, namely, that selection within a pure line is without effect.

But with *Difflugia*, another protozoan that secretes for itself a jug-like shell, Jennings, after a characteristically careful and prolonged study, has a different story to tell. *Difflugia* proved to be a more favorable form to study than *Paramecium* because it has numerous distinctive shell characters which are all inheritable to a high degree but are unchanged by growth and environment during the life of the individual, although presenting variations from parent to offspring.

Jennings selected for (1) the number of spines on the shell; (2) the length of the spines; (3) the diameter of the shell; (4) the depth of the shell; (5) the number of teeth surrounding the mouth; (6) the diameter of the mouth. In two families, "one (#303) including 495 descendants of a single individual, and the other (#314) including 1049 descendants of the original parent, selection was effective."

C. PARTHENOGENETIC PROGENY

Parthenogenetic animals furnish even better material than unisexual clonal animals for testing the effectiveness of selection in an unmixed line but here again the

conclusions of the investigators are not in entire harmony. There is no doubt that in most cases selection within a parthenogenetic line is futile although Banta's long continued observations upon daphnids seem to furnish evidence of an opposite kind. Particular weight should be given to this work because it presents one of the longest pure lines that ever passed under the seeing eye of a scientist. In some of his lines there have been 450 generations (1921) forming an unbroken line extending over 10 years' time. If this pedigree were translated into human generations of 30 years each it would make a period of 13,500 years and would run back over 100 centuries B. C. long before the very beginnings of human history. There is no doubt that many experiments in selection cannot be considered decisive because they concern altogether too few generations, as compared with the time that has been at the disposal of nature in accomplishing evolutionary change.

D. HOMOZYGOUS CROSSES

It is very difficult to find instances among animals and plants where two individuals are homozygous in all particulars. The nearest approach is "identical twins" which arise from a single fertilized egg and consequently are more nearly germinally alike, and can never cross since they are always of the same sex.

It is useful, nevertheless, to consider pure lines resulting from homozygous crosses *when limited to a single character rather than to individuals*, for of this condition there are numberless instances.

a. *Tower's Potato-Beetles*

As an illustration of the effect of selection within pure lines may be mentioned Tower's exhaustive experiments on the Colorado potato-beetle *Leptinotarsa decemlineata*. These beetles had been inbred for such an extended period that they were presumably homozygous for the character of color. Among the numerous cultures which were under control, a considerable variation in color, nevertheless, made its appearance. For convenience in classification these variations were graded into arbitrary classes or *graduated variants* ranging from dark to light.

When a male and a female from the extreme class at the dark end of the series were allowed to breed together, their progeny were not dark, but fluctuated in color around the original average of the entire series. The process of selecting each time an extreme pair of dark parents was continued for twelve generations, as shown in Figure 31, without in any way increasing the percentage of brunette potato-beetles in the progeny.

Thus in a pure line formed by the breeding of two individuals, alike with respect to color, the selection of an extreme variant was quite without effect in modifying the color of the progeny.

b. *Drosophila Bristles*

Among the "hairs" on the scutellum of *Drosophila melanogaster* there are four larger hairs or bristles, as shown in Figure 32.

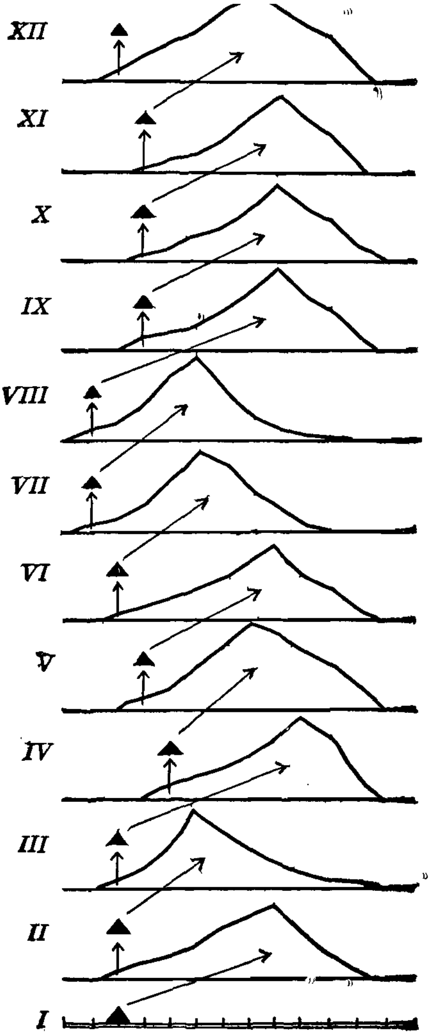


FIG. 31.—Diagram showing the ineffectiveness of selection through twelve generations within a homozygous strain in the case of the Colorado potato-beetle (*Leptinotarsa*). In each generation extremely dark specimens were selected as the parents of the succeeding generation but the progeny always swung back to the type. After Tower.

These four bristles are ordinarily strictly accounted for in heredity but the occasional variation in their number led MacDowell, and later others, to attempt to establish by selection a new style in these bristly decorations consisting of either extra or fewer bristles. Apparent success was the result in effective selection among the offspring of parents homozygous for the single character of four bristles.

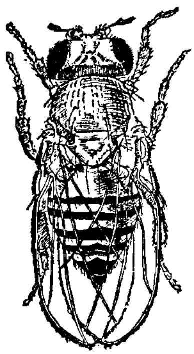


FIG. 32.–*Drosophila melanogaster*, the biological Cinderella. Drawn from Bridges by C. J. Fish.

c. Pearl's Egg-laying Hens

In an experiment extending over 17 years and which involved nearly 5000 pedigreed birds, Pearl tried, within a homozygous strain, to select a hen that would produce 200 eggs annually instead of the ordinary number of 125, but without success.

d. Castle's Hooded Rats

Finally one of the most famous selection experiments on record is that of extent of pigmentation, plus and minus, in the hooded rat. This experiment involved breeding an average of nearly twelve rats a day without cessation for eight years and it has not only made the Pied Piper of Hamelin roll over in his grave but has kept biologists busy with explanations of the results, for, like the four bristles on Drosophila's back, it ap-

parently furnishes evidence of modifications of an hereditary characteristic through selection following a homozygous cross.

Castle succeeded in selecting two extreme races of rats from his hooded stock, one possessing almost no pigment and the other with the "hood" so extended that it covered practically the entire body.

Is then the germ a variable thing that makes it possible to select effective differences out of a pure line, to the discomfiture of Mendelians who build their house on the rock of constancy of the germplasm, or can these perplexing results be somehow explained?

7. Conclusion

At any rate it would be gratifying scientifically to discover one fundamental law to which all these various cases of pure line selection are accountable because intellectual satisfaction always follows upon finding the common denominator of things.

A unifying explanation that makes a single harmonious interpretation of these apparently diverse results, based on the idea that all are reducible to Johannsen's conception of the *ineffectiveness of selection within a pure line*, has perhaps been reached in the *theory of modifying genes* which will be considered in the next chapter.

Certainly the pure line concept is a very useful tool for the geneticist since with it the hereditary upset of outside germplasm is eliminated. Consequently it is

of the utmost importance to know what can be done with this tool. In any event the way of experimentation and observation still lies open and what remains undiscovered makes life worth living.

CHAPTER VII

THE FACTOR HYPOTHESIS

1. The Hereditary Unit

In reducing any body of facts to a science, it is first necessary to determine the underlying units out of which the facts are made up.

Chemistry was alchemy until the chemical elements were identified and isolated. Histology was *terra obscura* until the cell theory brought forward "cells" as the units of tissues. In the same way there could be no science of genetics until the conception was developed that the individual is a bundle of unit characters rather than a unit in itself. So it has come about that geneticists speak of inheritance as applied to unit characters rather than to individuals as a whole.

The apparent somatic unit characters, like the color of the seed-coat or the length of the vine in Mendel's peas, are conditioned by other intangible but nevertheless real germinal units or determiners which give rise to them. Mendel was apparently unaware of the existence, in certain cases at least, of compound determiners. His experiments led him to believe that each character depends upon only a single determiner for the reason that he worked on characters severally belonging to different parts of the plant, but it has

been ascertained within the last decade that some characters require more than a single germinal determiner to bring them to somatic expression. The converse is also true, namely, that certain single determiners may control more than one character. For instance, the determiner for gray hair in rats also produces a lighter color on the belly.

The idea of compound germinal determiners for a single character has been termed the *factor hypothesis* of heredity.

Hereditary germinal factors, that may sometimes need to combine in order to produce a visible somatic unit character, are known as *genes* (Johannsen).

2. Different Kinds of Genes

There are various kinds of genes that bring about the visible expression of unit characters in various ways. An attempt to tabulate the kinds of genes is herewith given.

- SINGLE
  - *Alternative*
    - Allelomorphic
    - Presence or absence
- PLURAL
  - *Cumulative*
  - *Modifying*
    - Complementary
    - Supplementary
    - Lethal.

When genes are derived from two parents, as in all cases of sexual reproduction, they are always in pairs,

that is, one from each parent, and in the production of a unit character they may act in *single* or in several pairs.

If a single pair, the genes may be interpreted according to either the allelomorphic or the presence-or-absence hypothesis. In the first instance it is either one thing or an alternative that produces the character. For example, as in the case of the pea-vine, it is either tallness or dwarfness. In the second instance, the determiner of the character either *is* present or it *is not*, and the resulting unit character is dependent upon which of these two possibilities obtains. That is, applied to the illustration just given, if the hereditary factor or gene for tallness is present the pea-vine will be tall but if there is no gene for tallness the plant will be a dwarf. This condition is expressed by the term *alternative genes* and the operation of alternative genes follows in the typical Mendelian fashion described in Chapter V.

Under various kinds of plural determiners which involve more than one pair of genes, *cumulative genes* are those that are all alike in their separate effects but which, acting together, alter the degree of expression that is given to the unit character. These will be more fully described in Chapter VIII upon "Blending Inheritance."

Modifying genes are those germinal factors that are without effect alone but which in conjunction with other factors produce an alteration of those factors. They may be (1) *Complementary,* when a factor is added to a dissimilar factor in order that a particular charac-

ter may appear; (2) *Supplementary,* when a factor is added to a dissimilar factor already effective, with the result that a character is modified or changed in some way; (3) *Lethal,* so-called since they "cause the early death of those gametes or zygotes in which such a factor is not balanced by a normal one" (Conklin).

It will be profitable to consider a few illustrations of the factor hypothesis in some detail since it helps to explain both the reappearance of old types and the formation of new ones.

3. Complementary Genes

In the course of numerous breeding experiments Bateson obtained two strains of white sweet peas, *Lathyrus,* which, when normally self-fertilized, each bred true to the white color. When these two strains were artificially crossed, however, the progeny all had purple flowers like the wild ancestral Sicilian type of all cultivated varieties of sweet peas.

Here was apparently a typical instance of "reversion" which would have delighted Darwin's heart, but according to the factor hypothesis the true explanation is this. The character of purple color is dependent upon two independent genes which, though separately heritable, are both required to produce it. Each of these white strains of sweet peas possesses one of these genes which can produce colored flowers only when united with its complement, a proof of which appeared upon interbreeding hybrid purples from such a cross. In short, the color purple depends upon the action of

two complementary genes that follow the behavior of a dihybrid. (See Chap. V, par. 10.)

The gametic formulæ for the two strains of white sweet peas used in this experiment are *Cp* and *cP*,

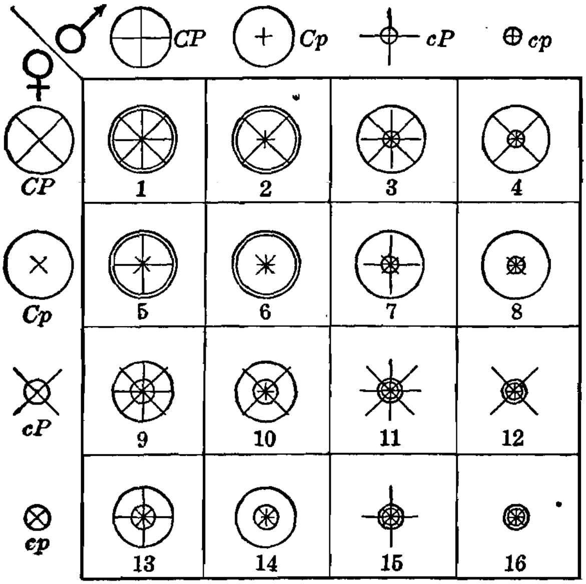


FIG. 33.—Diagram to illustrate the possible progeny from two heterozygous purple sweet peas according to data from Bateson. *C*, color gene (large circles); *c*, absence of *C* (small circles); *P*, pigment gene (large crosses); *p*, absence of *P* (small crosses). In the zygotes within the checkerboard squares the gametic symbols are superimposed.

respectively. *C* stands for a color gene without which no color can appear, and *c* is the absence of this factor, while *P* represents a purple pigment gene which finds expression in the somatoplasm only when taken together with the color gene *C*. The small letter *p*

stands for the absence of the purple pigment gene. It will be seen that each of the white sweet peas the formulæ of which are given above lack one of the two essential factors for purple color. When the two are crossed, however, all the progeny are purple with the formula *CcPp*.

These hybrid sweet peas upon gametic segregation theoretically produce four kinds of gametes, *CP*, *Cp*, *cP*, and *cp* which may combine as any other dihybrid in sixteen different ways. In this case, however, these combinations group themselves into only two phenotypes, purple and white, as indicated in the accompanying diagram (Fig. 33) in which *C* and *c* are represented by large and small circles respectively, while *P* and *p* are correspondingly indicated by large and small crosses. The gametic symbols are superimposed to form the zygotes.

The theoretical expectation here shown was closely approximated in the actual results.

It may be noted in passing that the seven kinds of white sweet peas resulting from the above cross, while phenotypically alike, that is, in the zygotic symbols of Figure 33, lacking either the large circle (color) or the large cross (pigment), belong to three distinct groups of genotypes as follows:—

		Number of Zygote in Figure 33
1	Without the pigment gene (large cross)	6 . 8 . 14
2	Without the color gene (large circle)	11 . 12 . 15
3	Without either pigment (large cross) or color (large circle)	16

Among the purple flowers are the following four genotypes:—

		Number of Zygote in Figure 33
1	Duplex for both color (large circle) and pigment (large cross)	1
2	Duplex for color (large circle) but simplex for pigment (large cross)	2 : 5
3	Simplex for color (large circle) but duplex for pigment (large cross)	3 : 9
4	Simplex for both color (large circle) and pigment (large cross)	4 · 7 : 10 · 13

4. Supplementary Genes

a. castle's agouti guinea-pigs

An illustration of a *supplementary gene* that acts only in conjunction with some other to bring about a modification, is the *pattern gene* demonstrated by Castle in his guinea-pigs.

The wild gray, or "agouti," color of the hair of certain guinea-pigs is due to the fact that pigment is distributed along the length of each hair in a definite pattern. The tip of a single hair is black followed by a band of yellow, while most of the proximal part which is more or less concealed by overlapping hairs is a leaden color. The distribution of pigment in such a pattern gives the characteristic gray, or agouti color to the coat when taken as a whole.

Castle demonstrated the separate nature and behavior of such a pattern gene when he discovered that

it is transmitted *independently of pigment,* which is necessary to bring it to expression. He showed that upon crossing a solid black guinea-pig, unquestionably possessing pigment but no "pattern," with a white albino guinea-pig having no pigment, some of the offspring "reverted" to the ancestral agouti, or "pattern" type, thus proving that the pattern must be carried in this case by the white or albino guinea-pig as a factor independent of the color which is necessary for its expression.

B. CUÉNOT'S SPOTTED MICE

Another instance of the interaction of supplementary genes is seen in the spotting of piebald mice. Cuénot discovered that such spotting is due to the absence of a *uniformity gene* which if present causes color to be uniformly distributed over the entire coat.

Both of these independent genes, spotting and uniformity, are real and not imaginary, since they may be separately transmitted through albino animals in the same way as the pattern gene mentioned above, notwithstanding that in albinos both are hidden through the absence of pigment, upon the presence of which their visibility depends.

Whenever piebald or spotted animals appear in a progeny derived originally from self-colored stock, it is evidently due to the absence of such a "uniformity" gene as has just been described.

Galton's theory of "particulate inheritance" (page 94) is now satisfactorily explained as true alterna-

tive inheritance in which the mosaic appearance is caused by a Mendelian determiner, in this instance a spotting gene or, in other words, the absence of a gene for uniformity.

C. MISS DURHAM'S INTENSIFIED MICE

Miss Durham, in her work with mice, has demonstrated an *intensifying gene*, the absence of which she calls a *diluting gene*. The action of the former produces, as its name implies, intensity of color, while that of the latter serves to lessen the degree of intensity in which color appears.

These genes of intensity and diluteness, it should be observed, do not in any way correspond to the duplex and simplex condition of a dominant color character, either of which would straightway appear if crossed with an albino. The factors of intensity and dilution of color are of an entirely different nature, as they have been proven to be independently transmissible through albinos where a color character could not appear because of the absence of pigment.

The following illustration of this kind of supplementary genes taken from Miss Durham's experiments will serve to make the case clear. The symbols employed are:—

B = *black* pigment which masks brown, or chocolate.
b = the absence of B, consequently *chocolate*.
I = intensity gene.
i = dilution gene or absence of intensity.
C = a complementary color gene acting with P.
P = a complementary pigment gene acting with C.
$BICP$ = black.

BiCP = blue or maltese (dilute black).
bICP = chocolate.
biCP = silver-fawn (dilute chocolate).

The results of crossing the hybrids formed from the ombinations indicated at the left in the table below are hown at the right where the expectation is given in arentheses after the actual results.

	Black (*BICP*)	Blue (*BiCP*)	Chocolate (*bICP*)	Silver-fawn (*biCP*)
Black (*BICP*) × Silver-fawn (*biCP*)	9(9)	4(3)	3(3)	2(1)
Blue (*BiCP*) × Chocolate (*bICP*) ..	42(45)	16(15)	14(15)	8(5)
Blue (*BiCP*) × Silver-fawn (*biCP*) .	0(0)	33(36)	0(0)	12(12)

It will be seen that the actual results, even when such small totals are concerned, approximate very closely the expectation and are entirely consistent.

D. CASTLE'S BROWN-EYED YELLOW GUINEA-PIGS

Furthermore Castle has shown that in guinea-pigs there is an independent gene for *extension* of pigment distinct from the uniformity gene already mentioned. The absence of this extension gene ("restriction") is manifested by a lack of black or brown pigment everywhere except in the eyes and to a slight extent in the skin of the extremities, ***while the distribution of yellow is wholly unaffected by it.***

That such "extension" and "restriction" genes really exist, is proven in the following way:—

When a brown (chocolate) guinea-pig is crossed with an ordinary black-eyed yellow one, the young are all black pigmented, but by cross-breeding these hybrid

young four varieties are obtained in the next generation, viz., black, brown, black-eyed yellow, and *brown-*

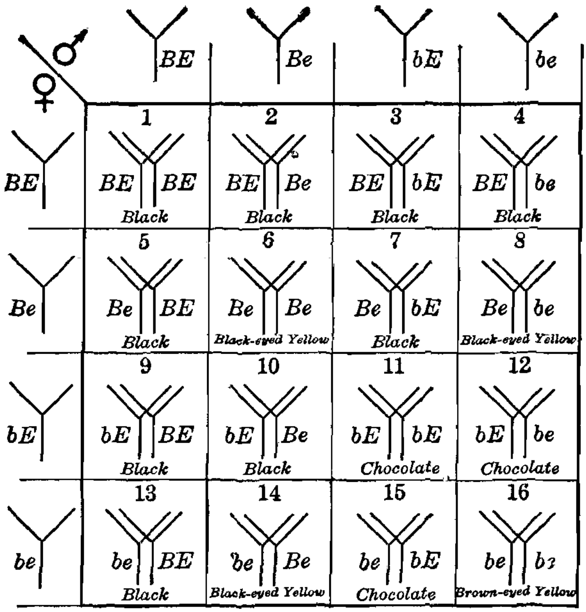


FIG. 34.—Diagram to illustrate the origin of a brown-eyed yellow guinea-pig from two heterozygous black parents, based upon Castle's experiments. The gene for yellow (*Y*) is present in every gamete and is consequently duplex in every zygote but is hidden whenever the gene *B* is present. *B*, black pigment hiding brown or chocolate; *b*, chocolate (absence of *B*); *E*, extension of *B* over the entire body hiding *Y*; *e*, restriction of *B* to eyes alone thus exposing *Y* over the entire body.

eyed yellow, the latter a variety unknown before Castle's experiment in breeding was made.

For the sake of clearness the formation of the brown-eyed yellow is shown above in Figure 34.

Symbols

B = *black pigment, hiding brown or chocolate.*
b = absence of B, or *chocolate.*
Y = yellow pigment, hidden by B.
E = extension of B over entire body, hiding Y.
e = restriction of B to eyes alone, thus exposing Y over the entire body.
C = complementary color gene acting with P to produce color.
P = complementary pigment gene acting with C to produce color.
(The genes C and P may be omitted for the sake of simplicity, since they are present in each instance.)

First Cross

"Extended" chocolate (bEY) × black-eyed yellow (BeY) = black ($BbEeYY$).

Second Cross

When these cross-breds are mated with each other, they each form four kinds of gametes, BEY, BeY, bEY, and beY, which unite into sixteen theoretical genotypic possibilities, some of which are unlike (Fig. 34). These fall into four phenotypes, nine black (BEY), three black-eyed yellow (BeY), three chocolate (bEY), and one brown-eyed yellow (beY). The actual results in Castle's experiments gave all four kinds in close numerical agreement with this expectation. The action of extension and restriction genes is, therefore, plainly a case of Mendelian dihybridism in which two independent pairs of alternative characters are concerned.

E. RABBIT PHENOTYPES

Perhaps no better application of the factor hypothesis, so far as supplementary genes are concerned, may be found than in the case of the color of rabbits.

There are many varieties of rabbits with respect to color, particularly among domesticated races. These varieties are now quite explainable by the factor hypothesis, as indicated in the table below. The sixteen kinds of rabbits there catalogued have been obtained by

THE FACTOR HYPOTHESIS APPLIED TO COLORS OF RABBITS

<table>
<tr><th colspan="3">CONSTANT GENES</th><th colspan="5">ALTERNATIVE GENES</th><th rowspan="2">GAMETIC FORMULA</th><th rowspan="2">PHENOTYPIC CHARACTER WHEN CROSSED WITH THE SAME KIND OF GAMETIC COMBINATION</th></tr>
<tr><th>1</th><th>2</th><th>3</th><th>4</th><th>5</th><th>6</th><th>7</th><th>8</th></tr>
<tr><td rowspan="16">Br</td><td rowspan="16">B</td><td rowspan="16">Y</td><td rowspan="16">C</td><td rowspan="8">E</td><td rowspan="4">I</td><td rowspan="2">U</td><td>A</td><td>AUIEC[YBBr]</td><td>Gray</td></tr>
<tr><td>a</td><td>aUIEC [YBBr]</td><td>Black</td></tr>
<tr><td rowspan="2">u</td><td>A</td><td>AuIEC [YBBr]</td><td>Gray spotted</td></tr>
<tr><td>a</td><td>auIEC [YBBr]</td><td>Black spotted</td></tr>
<tr><td rowspan="4">i</td><td rowspan="2">U</td><td>A</td><td>AUiEC [YBBr]</td><td>Blue-gray</td></tr>
<tr><td>a</td><td>aUiEC [YBBr]</td><td>Blue (Maltese)</td></tr>
<tr><td rowspan="2">u</td><td>A</td><td>AuiEC [YBBr]</td><td>Blue-gray spotted</td></tr>
<tr><td>a</td><td>auiEC [YBBr]</td><td>Blue spotted</td></tr>
<tr><td rowspan="8">e</td><td rowspan="4">I</td><td rowspan="2">U</td><td>A</td><td>AUIeC [YBBr]</td><td>Yellow (with white belly and tail)</td></tr>
<tr><td>a</td><td>aUIeC [YBBr]</td><td>Sooty yellow (with yellow belly and tail)</td></tr>
<tr><td rowspan="2">u</td><td>A</td><td>AuIeC [YBBr]</td><td>Yellow spotted</td></tr>
<tr><td>a</td><td>auIeC [YBBr]</td><td>Sooty yellow spotted</td></tr>
<tr><td rowspan="4">i</td><td rowspan="2">U</td><td>A</td><td>AUieC [YBBr]</td><td>Cream</td></tr>
<tr><td>a</td><td>aUieC [YBBr]</td><td>Pale sooty yellow</td></tr>
<tr><td rowspan="2">u</td><td>A</td><td>AuieC [YBBr]</td><td>Cream spotted</td></tr>
<tr><td>a</td><td>auieC [YBBr]</td><td>Pale sooty yellow spotted</td></tr>
</table>

Castle and other experimental breeders, as well as many of the albino types that would double this list if *c*, or the gene for absence of color, should be substituted for *C*, the presence of color, in column 4 of the table on page 160.

Explanation of Symbols in the Foregoing Table

Br = a gene acting on *C* to produce *brown* pigmentation.
B = a gene acting on *C* to produce *black* pigmentation.
Y = a gene acting on *C* to produce *yellow* pigmentation.
The three genes, *Y, B, Br*, are present in every rabbit gamete and up to date have not been separable as independent unit characters, although they have been separated out in guinea-pigs and mice. There are no brown rabbits, because black always goes linked with brown covering the brown factor. Yellow rabbits result, as explained below, through the action of factor *e*.
C = a common *color* gene necessary for the production of any pigment. It was discovered in 1903 by Cuénot.
c = the absence of *C* which results in albinos, regardless of whatever pigment gene may be present. By changing *C* to *c*, sixteen kinds of albinos would be added to this catalogue, an addition of one phenotype and sixteen genotypes, all looking alike but breeding differently.
E = a gene governing the *extension* of black and brown pigment, *but not of yellow*.
e = the absence of extension or *restriction* of black and brown pigment to the eyes and the skin of the extremities only, while yellow remains extended and visible. Demonstrated by Castle in 1909.
I = an *intensity* gene which determines the degree of pigmentation. It can be transmitted independently of *C* through an albino. Discovered by Bateson and Durham in 1906.
i = the absence of intensity or *dilution*. Dilute black = blue. Dilute yellow = cream. Dilute gray = blue-gray.
U = a gene for uniformity of pigmentation or "self-color" discovered by Cuénot in 1904.
u = the absence of uniformity which results in *spotting with white*.
A = a pattern gene for agouti, or wild gray color, which causes the brown and black pigments to be excluded from certain portions of each hair, resulting in the gray coat. When present in the rabbit, it is also associated with white or lighter color on the under surfaces of the tail and belly. It was demonstrated by Castle in 1907.
a = the absence of the agouti or pattern gene.

F. THE KINDS OF GRAY RABBITS

Each of the apparent kinds of gray rabbits indicated in the foregoing table may be made up of various genotypes. For instance, there are thirty-two different genotypes, each of which is phenotypically a gray rabbit. The zygotic formula for each of these thirty-two possibilities is displayed in the next table, and it will be seen that these range all the way from rabbits homozygous in all their variable characters (No. 1) to those homozygous in none (No. 32).

The progeny of these various types of gray rabbits when inbred will consequently vary from the pure gray, as in No. 1, to a gray from which sixteen possible types of young may be expected as in No. 32.

Up to the time when Castle's paper upon the factor hypothesis[1] was published in 1909, nine genotypic kinds of gray rabbits had been obtained in his experiments, whose genotypic formulæ correspond to the following numbers in the list: 1, 3, 6, 10, 13, 20, 22, 28, 29.

5. Lethal Genes

Among mammals, as shown by Cuénot and confirmed by Little, homozygous or pure yellow mice are unknown although yellow individuals have long been exploited by fanciers. In other words, all kinds of yellow mice behave as if heterozygous or simplex with respect to yellow color, for when any two yellow mice

[1] "Studies of Inheritance in Rabbits." Carnegie Institution Publications, No. 114, 1909. W. E. Castle in collaboration with Walter, Mullenix and Cobb.

THE KINDS OF GRAY RABBITS (Color only)

	Genotype Zygotic Formula	Number of Heterozygotic Factors	Gray	Black	Gray spotted	Black spotted	Blue gray	Blue	Blue gray spotted	Blue spotted	Yellow	Sooty	Yellow spotted	Sooty spotted	Cream	Pale sooty	Cream spotted	Pale sooty spotted	White
			Phenotypes: When inbred, these kinds are produced																
1	*AAUUIIEECC* [*YBBr*] [*YBBr*]	None	×																
2	*AAUUIIEECc* [*YBBr*] [*YBBr*]	One	×																×
3	*AAUUIIEeCC* [*YBBr*] [*YBBr*]	One	×								×								
4	*AAUUIiEECC* [*YBBr*] [*YBBr*]	One	×				×												
5	*AAUuIIEECC* [*YBBr*] [*YBBr*]	One	×		×														
6	*AaUUIIEECC* [*YBBr*] [*YBBr*]	One	×	×															
7	*AAUUIIEeCc* [*YBBr*] [*YBBr*]	Two	×								×								×
8	*AAUUIiEECc* [*YBBr*] [*YBBr*]	Two	×				×												×
9	*AAUuIIEECc* [*YBBr*] [*YBBr*]	Two	×		×														×
10	*AaUUIIEECc* [*YBBr*] [*YBBr*]	Two	×	×															×
11	*AAUUIiEeCC* [*YBBr*] [*YBBr*]	Two	×				×				×				×				
12	*AAUuIIEeCC* [*YBBr*] [*YBBr*]	Two	×		×						×		×						
13	*AaUUIIEeCC* [*YBBr*] [*YBBr*]	Two	×	×							×	×							
14	*AAUuIiEECC* [*YBBr*] [*YBBr*]	Two	×		×		×		×										
15	*AaUUIiEECC* [*YBBr*] [*YBBr*]	Two	×	×			×	×											
16	*AaUuIIEECC* [*YBBr*] [*YBBr*]	Two	×	×	×	×													
17	*AaUuIiEECC* [*YBBr*] [*YBBr*]	Three	×	×	×	×	×	×	×	×									
18	*AaUuIIEeCC* [*YBBr*] [*YBBr*]	Three	×	×	×	×					×	×	×	×					
19	*AaUuIIEECc* [*YBBr*] [*YBBr*]	Three	×	×	×	×													×
20	*AaUUIiEeCC* [*YBBr*] [*YBBr*]	Three	×	×			×	×			×	×			×	×			
21	*AaUUIiEECc* [*YBBr*] [*YBBr*]	Three	×	×			×	×											×
22	*AaUUIIEeCc* [*YBBr*] [*YBBr*]	Three	×	×							×	×							×
23	*AAUuIiEeCC* [*YBBr*] [*YBBr*]	Three	×		×		×		×		×		×		×		×		
24	*AAUuIIEeCc* [*YBBr*] [*YBBr*]	Three	×		×						×		×						×
25	*AAUuIiEECc* [*YBBr*] [*YBBr*]	Three	×		×		×		×										×
26	*AAUUIiEeCc* [*YBBr*] [*YBBr*]	Three	×				×				×				×				×
27	*AAUuIiEeCc* [*YBBr*] [*YBBr*]	Four	×		×		×		×		×		×		×		×		×
28	*AaUUIiEeCc* [*YBBr*] [*YBBr*]	Four	×	×			×	×			×	×			×	×			×
29	*AaUuIIEeCc* [*YBBr*] [*YBBr*]	Four	×	×	×	×					×	×	×	×					×
30	*AaUuIiEECc* [*YBBr*] [*YBBr*]	Four	×	×	×	×	×	×	×	×									×
31	*AaUuIiEeCC* [*YBBr*] [*YBBr*]	Four	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
32	*AaUuIiEeCc* [*YBBr*] [*YBBr*]	Five	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×

are bred together they produce a certain percentage of recessives lacking yellow which would not happen if they were pure yellow. Hundreds of yellow individuals have been tested but they always produce in addition to yellow some non-yellow, that is, black, brown or gray individuals. That the non-yellow individuals are recessive is shown by the fact that when inbred, they produce no yellow offspring, therefore, yellow is dominant.

In a Mendelian monohybrid cross, as has been previously pointed out, the expectation is that in the second generation one fourth of the offspring will be recessives ($DR \times DR = DD + 2\,DR + RR$), but when yellow mice are bred together, the percentage of recessives approximates one-third instead of one-fourth. Little, in a total of over 1200 young produced by yellow parents, obtained almost exactly two-thirds yellow. This apparent exception to the Mendelian ratio finds an explanation, however, when it is assumed that *D* (yellow) is a *lethal gene when present in duplex* (*DD*) *form*. The *DD*s drop out entirely which leaves the proportion approximately two *DR*s and one *RR*. This supposition is further supported by the fact that the litters of young from yellow mice are, on an average, only three-fourths as large as normal litters of mice, which is exactly what would be expected if one-fourth of the possible gametic combinations (*DD*) fail to produce offspring. Moreover, evidence of the death *in utero* of the pure yellow mice has been produced by Ibsen and Stiegleder, '17.

Morgan and his associates have demonstrated the existence of over twenty different lethal factors in *Drosophila* which when inherited from both parents not only prevent the development of any unit characters but also doom the individual to death. Only heterozygotes for such lethals, who receive the death warrant from one parent alone, may escape and hand on this fatal determiner.

In plants lethal genes have been demonstrated by Baur in snapdragons and by Lindstrom in maize. In these instances the lethal factor is a lack of chlorophyll which is not fatal if inherited from a single parent because the deficiency is supplied by a gene for chlorophyll from the other parent, but when the lack comes from both parents it produces a seedling unable to survive.

Recently G. H. Shull has demonstrated the existence of two balanced recessive lethal factors in one pair of the fourteen chromosomes in *Œnothera*, one pair producing a lethal effect *in the zygote*, the other pair *destroying the gametes*. This fact explains many of the hitherto confusing ratios obtained in breeding this classical plant.

"Such lethal factors modify the expected Mendelian ratios and greatly complicate the study of genetics, but they do not destroy its fundamental principles, indeed when properly understood they furnish one of the strongest proofs of the truth of the factorial theory of heredity" (Conklin).

6. Modifying Genes and Selection

The recognition of modifying genes has furnished an explanation for the apparent effectiveness of selection within a pure line without assuming germinal inconstancy.

The gene itself, like that producing the hooded pattern of Castle's rats, is *constant* but it is accompanied by a halo of modifying genes likewise constant which have no somatic expression except when the original factor for hooded pattern is present. These modifying genes are simply potential increasers or diminishers of the hooded-pattern gene. In the absence of the pattern gene there is nothing to increase or diminish and consequently there is no way to demonstrate the modifying factors. They are not imaginary things, however, for their separate existence and transmissibility have been demonstrated from many sides. What selection within the progeny of the homozygous cross of hooded rats or bristly flies accomplishes is simply the elimination or addition of either plus or minus modifying genes, according as the attempt is being made to increase or decrease the hooded pattern of pigmentation or the number of bristles.

If this explanation stands the test of further investigation then we are still dealing in heredity with constant dependable units, such as the chemist finds in his elements, and it may be said that all genetic roads lead to the Rome of *gene-constancy.*

However, it is well to remember that Darwin did not revolutionize the concept of evolution until he broke

down the idea of constancy of species and that geology did not come into its own until Lyell substituted for constancy the molding hand of incessant change.

No doubt there is a substratum of unity underlying all of these processes and Mendelians, therefore, may still retain their constant characters undismayed and have, at least, the three following ways left by means of which it is possible to get results in selection:—

(1) By the isolation of pure lines if the stock is hybrid (heterozygous);

(2) By the elimination or addition of modifying genes if the stock is pure (homozygous);

(3) By mutation of the genes.

It should be repeated that change by mutation does not beg the question of constancy of the genes. A mutation is not a changed gene. It is the substitution of an entirely different one.

CHAPTER VIII

BLENDING INHERITANCE

1. Relative Significance of Dominance and Segregation

Of the three fundamental principles which underlie "Mendel's law," namely, segregation, independence of unit characters, and dominance, the principle of dominance has been found to hold true in a surprising number of cases and in relation to very diverse organisms, notwithstanding the fact that its universal application is by no means assured.

Mendel himself noted certain exceptions to the law of dominance, and his followers have pointed out with increasing emphasis that it is subject to many modifications. It is now understood, indeed, that *segregation, not dominance,* is the most essential factor in the Mendelian scheme.

2. Imperfect Dominance

It frequently occurs that dominance is so imperfect that a heterozygous, or simplex, dominant may be distinguished at once by simple inspection from a homozygous, or duplex, dominant, whereas the test of crossing with a recessive is necessary whenever dominance is complete, as has been previously explained. The

single dose of the determiner in such a case has plainly, then, less phenotypic effect than a double dose.

There are many instances of imperfect dominance among flowering plants. Correns' red and white four-o'clocks with pink offspring (p. 106) is a case in hand.

A classic illustration of imperfect dominance among animals is the "blue Andalusian fowl," the hereditary behavior of which is illustrated below (Fig. 35). It will be seen that when two blue Andalusian fowls,

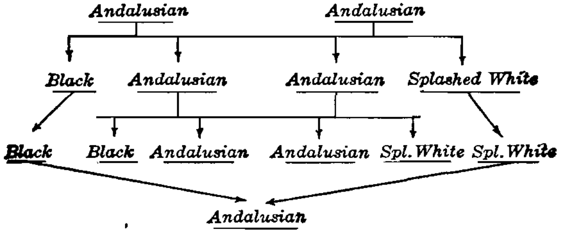


FIG. 35.—The heredity of the blue Andalusian fowl, an illustration of "imperfect dominance."

characterized by a mottled plumage, are bred together, they produce three kinds of offspring in the ratio of 1 : 2 : 1. Twenty-five per cent are clear black, 50 per cent are blue Andalusian, and 25 per cent are white "splashed" with black. Both the black and the splashed white fowls from this cross prove, upon further breeding, to be homozygous, while the blue Andalusian itself is heterozygous and can, therefore, never be made to breed true. In order to produce 100 per cent of blue Andalusian chicks, it is necessary simply to cross a splashed white with a black Andalusian.

There is nothing in this case to indicate whether the

black or the splashed white should be regarded as the homozygous dominant, since dominance is imperfect. In either case the heterozygous blue Andalusian is at once evident in the first filial generation without further crossing.

A similar case of imperfect dominance is furnished by the roan color of cattle which results when red and white are crossed. If two roans are mated, they produce red, roan, and white offspring in the proportion of 1 : 2 : 1, thus showing that roan is a heterozygous character in which the dominance of red is imperfect.

Even in cases of apparently perfect dominance it is sometimes possible by close inspection to detect differences between a pure dominant (*DD*), Figure 17, and a heterozygous dominant (*DR*) when a superficial examination is not sufficient to distinguish them.

Morgan cites a *Drosophila* cross between "ebony" and "sooty" wings wherein the F_2 generation ranges from ebony to sooty in an inseparable transition but it proves, nevertheless, to be of three classes in the proportion of 1 : 2 : 1, as further breeding tests show.

3. Delayed Dominance

A character which is really dominant is sometimes so late in manifesting itself in the individual growth of the offspring that it may properly be termed a *delayed dominant.*

Dark-haired individuals often do not acquire their definitive hair color until adult life, and it is common knowledge that the eyes of an infant for a consider-

able period provoke no little speculation among adoring relatives as to "whose eyes" they are.

According to Davenport, when a white Leghorn fowl is crossed with a black Leghorn, white being dominant in this case, chicks are produced that are *white with black flecks in their plumage.* These black flecks, however, disappear at the time of the first molt. The complete dominance of white is, therefore, simply delayed.

4. "Reversed" Dominance

In certain instances there seems to be a reversal of dominance, as may be illustrated by Lang's results with snails (*Helix*). He has proven in his experiments that red snails are generally dominant over yellow snails, although in certain cases there is apparently an exception to the rule, for snails with yellow shells dominate those with red shells.

Davenport has shown too that although extra toes are usually dominant over the normal number in poultry, yet, in something like 20 per cent of the cases, the normal number is dominant.

It sometimes occurs that a character which is dominant in one species may be recessive in another. Horns are dominant in sheep, but recessive in cattle. White color is recessive in rodents and sheep, but dominant in most poultry and in pigs.

Again Morgan describes a *Drosophila* that possesses a gene for abnormally banded abdomen which does not come to somatic expression unless the flies are supplied with fresh food and a proper amount of moisture.

When the food becomes dried up and there is a minimum of moisture the banding on the abdomen disappears. Here is a reversal of dominance but the gene itself is not affected since the same flies which are hybrid with respect to the character of banding, show a difference according to the environment of food and moisture, in the amount of banding given expression.

Notched margin in leaves is dominant in nettles and recessive in the celandine. Again a negative character may be the dominant one in a pair of allelomorphs. For example, the bob-tail of the Manx cat is dominant over the ordinary long tail of the cat; the reduced number of three digits in guinea-pigs is dominant over four digits; the polled condition is dominant over horns in cattle; the rumpless fowl is dominant over the fowl with a rump, and brachydactyly in man, that is, fingers or toes with only two joints each, is dominant over the three-jointed arrangement.

5. Potency

Davenport seeks to explain modifications in typical dominance as variations in the *potency* of determiners. He defines potency as follows: "The potency of a character may be defined as the capacity of its germinal determiner to complete its entire ontogeny."

That is, if the potency of a determiner, for some reason, is insufficient, there may be either an incomplete or delayed manifestation of the character in question, or it may fail entirely to develop.

The variations of potency may be grouped into three

general categories according to the degree of their manifestation; namely, total potency, partial potency, and failure of potency.

A further word of explanation for each of these three kinds of potency seems desirable at this point.

A. TOTAL POTENCY

This is complete Mendelian dominance in which even the heterozygotes produced by a simplex dose of a character are indistinguishable phenotypically, that is, by inspection, from the homozygotes produced by a duplex dose of the same character. It is as if a single bottle of black ink poured into a jar of water was just as effective as *two* bottles of ink, in forming an opaque fluid.

Even in the cases of apparently complete dominance, however, refined methods of examination or analysis may make it possible to distinguish the duplex from the simplex condition without recourse to breeding. Darbishire has shown, in the case of Mendel's smooth and wrinkled peas, that the two kinds of smooth progeny from the F_1 hybrid upon microscopic examination show a difference in their starch grains that indicates at once which is homozygous and which is heterozygous. Moreover, in the power of absorption, hybrid smooth peas (*DR*) are intermediate between their pure dominant smooth (*DD*) and pure recessive wrinkled (*RR*) parents.

Blakeslee has demonstrated a chemical method of distinguishing unseen genetic differences in the appar-

ently similar flowers of the black-eyed susan (*Rudbeckia hirta*). When placed in a solution of KOH, the yellow cones of one kind turn a purplish-black, while the other kind turns red.

B. PARTIAL POTENCY

Partial potency covers all cases of *incomplete dominance*, such as those of the four-o'clock (*Mirabilis*) and blue Andalusian fowls, where a simplex dose of a determiner does not produce the same visible effect as a double dose.

The dominant prickly jimson weed (*Datura*), when crossed with a recessive glabrous variety of the same plant, produces cross-breds in the first generation which show only a few prickles (Bateson) (Baur), following the law of partial potency.

Banded and uniformly colored snails also, when crossed together, produce snails with shells showing only a pale banding (Lang).

Numerous further instances of incomplete dominance could be cited.

C. FAILURE OF POTENCY

If for any reason a determiner fails to accomplish its possibilities in whole or in part, then the character in question may never become evident, and the result, so far as appearances go, is the same as if it was a recessive lacking the determiner entirely.

That the failure of potency is not identical with the absence of a determiner can usually be demonstrated

by further breeding, because dominants failing in potency, which are either of the formula *DD* or *DR*, may, if bred *inter se*, give a various progeny among which the dominant character *D* is likely to become manifest again, while recessives, of the formula *RR*, on the contrary, will invariably give offspring which all agree in the entire absence of the character in question.

Davenport cites an extreme case of failure of potency in one of two rumpless cocks from the same blood. The character of rumplessness is due to an *inhibitor* of tail development. That these two cocks both possessed this character was demonstrated by the entire absence of any tail in either case. The inhibiting determiner for tail growth was so weak in cock No. 117, however, that, to quote Davenport's exact words: "In the heterozygote the development of the tail is not interfered with at all, and even in extracted dominants it interfered little with tail development, so that it makes itself felt only in the reduced size of the uropygium and in-bent or shortened back. But in No. 116 the inhibiting determiner is strong. It develops fully in about 47 per cent of all the heterozygotes and in extracted dominants may produce a family in *all* of which the tail's development is inhibited."

Here were two birds of the same blood, phenotypically alike and presumably genotypically alike, which because of an individual difference in the potency of the determiner for rumplessness produced quite different results in their offspring although bred to precisely the same array of hens.

6. Blending Inheritance

In the instances of imperfect dominance given above, where the progeny of unlike parents present an intermediate condition, it is found that, upon cross-breeding these offspring, segregation into the grandparental types occurs just as truly as in instances of complete dominance.

In poultry, for example, when Cochins, which are "booted," and Leghorns, which are clean-shanked, are crossed, booting of an intermediate grade of four results, on a scale in which ten represents complete booting, and zero, no booting or clean shank (Davenport). The character of booting and its alternative absence, however, segregate out in true Mendelian fashion when these hybrids are subsequently crossed together. It is evident that dominance plays only a secondary rôle in such cases, and that the all-important factor is segregation.

Are there, then, any cases where true fusion of hereditary parental traits occurs, in other words, where *segregation in the second filial generation does not appear?* Does the "melting-pot of cross-breeding" ever "melt" the characters thrown into it?

It was formerly believed that diverse parents generally *produce intermediate offspring, and that this* intermediate condition continues without any segregation at all in the form of "blending inheritance," but within the last decade apparent cases of blending inheritance have been thrown out of court one after the other by the Mendelians. Bateson, in an inaugural

address at Cambridge University in 1908, stated that what was once believed to be the rule has now become the exception. He goes on to say: "One clear exception I may mention. Castle finds that in a cross between the long-eared lop rabbit and a short-eared breed, ears of intermediate length are produced; and that these intermediates breed approximately true."

Let us examine this "one clear exception" a little more closely.

7. The Case of Rabbit Ears

As a typical example of blending inheritance in rabbit ears the following case may be cited:—

A female Belgian hare with an ear-length of 118 mm. was crossed with a male lop-eared rabbit with an ear-length of 210 mm. The average of these ear-lengths is 164 mm. Five offspring from this pair had ear-lengths, when adult, approximating this average as follows: 170, 170, 166, 156, 170, of which two were females and three were males. When from this litter one of the females measuring 170 mm. in ear-length was subsequently crossed with her brother having an ear-length of 166 mm., two litters were produced in which the individuals when adult attained ear-lengths of 170, 166, 168, 160, 172, and 168 mm. These results are represented diagrammatically in Figure 36.

This illustration is typical of many other breeding experiments made by the same investigators [1] upon the

[1] Castle, in collaboration with Walter, Mullenix and Cobb. "Studies of Inheritance in Rabbits." Carnegie Institution Publications, Washington, No. 114, 1909.

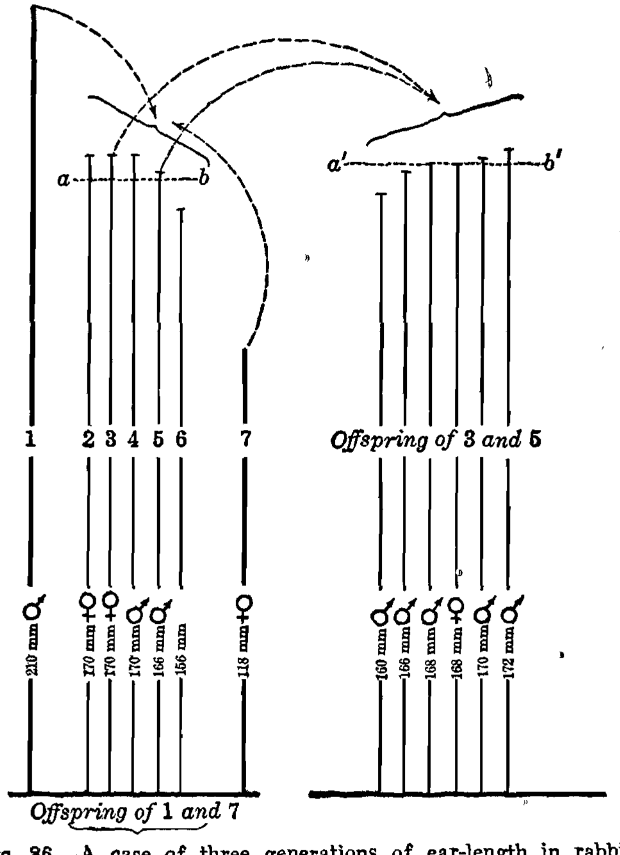


FIG. 36.—A case of three generations of ear-length in rabbits. *a-b*, average ear-length of the first filial generation (F_1). *a'-b'*, average ear-length of the F_2 generation derived from 1 and 7. Data from Castle, in collaboration with Walter, Mullenix and Cobb.

ear-length of rabbits which included 70 different litters of rabbits containing 341 individuals. In none of these experiments could the blend in the second filial genera-

tion be called perfect, but it may at least be said that evidence of segregation, that is, a return to one or the other of the parental types, was much less apparent than evidence of blending.

Furthermore, crosses were made in which lop ears of various fractional lengths were obtained as desired, including $\frac{1}{8}$, $\frac{1}{4}$, $\frac{3}{8}$, $\frac{1}{2}$, $\frac{5}{8}$, $\frac{3}{4}$, and $\frac{7}{8}$ lengths. Not one of these fractional lengths apparently segregated in subsequent generations after the Mendelian fashion, but all bred approximately true.

Moreover, ears of one half lop length, for instance, were obtained in three ways: first, by crossing full-length lops with short-eared rabbits as indicated in the first cross of the case cited above; second, by crossing one half lop lengths together, demonstrated by the second cross in the illustrative case given, and third, by mating $\frac{1}{4}$ and $\frac{3}{4}$ lop lengths. Theoretically, $\frac{1}{8}$ and $\frac{7}{8}$ as well as $\frac{3}{8}$ and $\frac{5}{8}$ lop lengths would also produce $\frac{1}{2}$ lop lengths, for in all of the crosses that were made the length of ear behaved in a blending fashion.

These results were based, not upon a single measurement of each specimen, which might be open to considerable error, but upon daily measurements from the time the rabbits were two weeks old until their ears ceased to grow at about twenty weeks. The growth curves drawn from these daily measurements showed continually an intermediate or blending condition in progeny derived from diverse parents.

A Mendelian explanation of this apparently exceptional case of blending inheritance has been suggested by Lang based upon the result of Nilsson-Ehle's dis-

coveries while breeding wheats at the Agricultural Experiment Station of Svalöf in Sweden.

8. The Nilsson-Ehle Discovery

Nilsson-Ehle, 1907, found in breeding together different strains of wheat that a certain wheat with brown chaff crossed with a white-chaffed strain yielded only brown-chaffed wheat in the first generation. These heterozygous or hybrid brown-chaffed wheats when crossed with each other produced, not the expected proportion of three brown to one white, but *fifteen brown to one white.* This was not explainable as the chance result of a single cross, but was the conclusion drawn from fifteen different crosses, all of the same strains, that yielded a total progeny of 1410 brown-chaffed to 94 white-chaffed plants, which happens to be exactly the proportion of fifteen to one.

In other experiments it was discovered that although dominant red-kerneled strains of wheat crossed with white-kerneled varieties usually gave the three-to-one proportion upon segregation in the second filial generation, yet *one particular strain* of red-kerneled Swedish wheat in the second generation gave approximately sixty-three red to one white-kerneled strain.

The explanation of these two unexpected results is this. In the case of brown-chaffed wheat there are two independent determiners for the character of brown color, and these simply follow the Mendelian laws for a dihybrid, while in the case of the red-kerneled wheat there are three independent determiners for the charac-

ter of red color, each of which is able to give red color to the wheat. Taken together, these three red color determiners behave *cumulatively*, following the law of a trihybrid.

For example, if a brown-chaffed wheat with the formula *BB′*, in which *B* and *B′* each represent a brown-chaffed factor, is crossed with a white-chaffed wheat of the formula *bb′*, in which *b* and *b′* each represent the absence of *B* and *B′* respectively, then all the progeny of this cross will be brown-chaffed, having the zygotic formula *BB′bb′*. When upon maturation the gametes form out of the germ-cells from such hybrids, the following four combinations are possible, and no others: *BB′*, *Bb′*, *bB′*, *bb′*. These represent, therefore, the possible gametes present in each sex of the first filial generation, and upon intercrossing they may combine into sixteen possible zygotes to form the second filial generation, as shown in Figure 37.

	BB′	*Bb′*	*bB′*	*bb′*
BB′	*BB′* *BB′* (4)	*Bb′* *BB′* (3)	*bB′* *BB′* (3)	*bb′* *BB′* (2)
Bb′	*BB′* *Bb′* (3)	*Bb′* *Bb′* (2)	*bB′* *Bb′* (2)	*bb′* *Bb′* (1)
bB′	*BB′* *bB′* (3)	*Bb′* *bB′* (2)	*bB′* *bB′* (2)	*bb′* *bB′* (1)
bb′	*BB′* *bb′* (2)	*Bb′* *bb′* (1)	*bB′* *bb′* (1)	*bb′* *bb′* (0)

FIG. 37.—Diagram of the possible combinations in the F_2 generation of brown-chaffed wheat according to experiments of Nilsson-Ehle. *B* and *B′* are cumulative factors for the brown-chaff character; *b* and *b′* denote the absence of *B* and *B′* respectively.

The numbers in the squares in Figure 37 indicate how many times a brown determiner is present in each zygote. It will be seen that only one out of the sixteen possibilities lacks a brown-chaff factor, and this one will

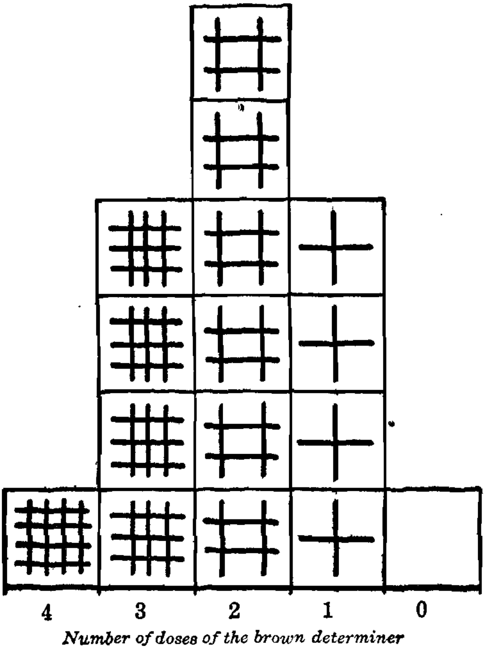


FIG. 38.—The distribution of the sixteen possibilities resulting when two similar determiners (brown-chaff) act together as a dihybrid.

consequently produce only white chaff, while the remaining fifteen possibilities, each of which has at least a single determiner for brown, will all yield brown chaff.

The brown-chaff factor, moreover, is present in

varying doses among these fifteen possibilities, as indicated by the numbers in the squares. It is evident, therefore, that several shades of brown will be repre-

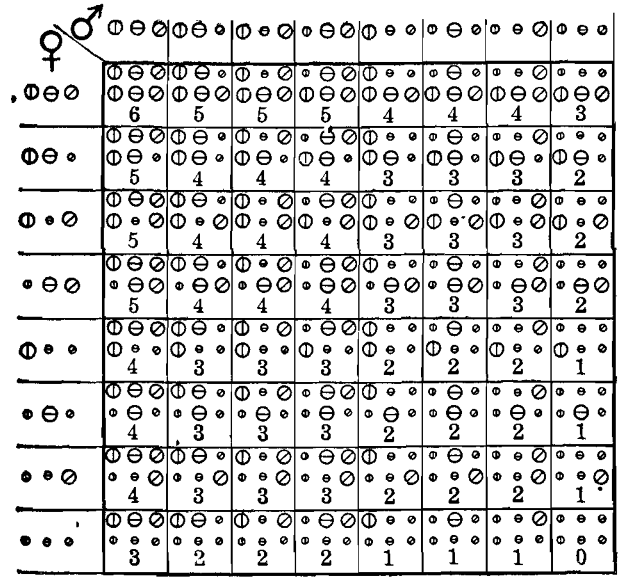


FIG. 39.—Diagram to illustrate Nilsson-Ehle's case of trihybrid red wheat. The large screw-heads each represent a single determiner for the red character. The small screw-heads symbolize the absence of the red character, or white. The number in each square indicates how many doses of the "red" determiner is present. For further explanation see text.

sented depending upon the number of doses of the brown determiner in each instance.

Figure 38 shows how these different shades of brown arrange themselves in the manner of a frequency curve of fluctuating variation with the greatest number in

the halfway class and the least numbers at the two extremes. In this instance six out of sixteen individuals of the second generation theoretically present a perfect "blend" between the original brown- and white-chaffed grandparents, although complete segregation has actually occurred.

The same explanation holds true as displayed in Figure 39 for the trihybrid case of red- and white-kerneled wheats in which only one white-kerneled to sixty-three red-kerneled individuals appear in the sec-

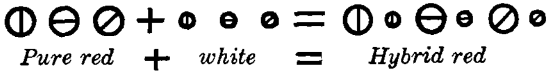


Fig. 40.—The result of crossing white wheat with trihybrid red wheat.

ond filial generation. The number of red determiners in each zygote is indicated by the figure at the bottom of each square. The large screw-head symbols with vertical, horizontal and diagonal slots each represent an independent determiner for red kernel, while the small screw-heads symbolize the absence of each of these determiners, or white kernel. When the pure strain of red-kerneled wheat is crossed with a pure strain of white-kerneled wheat, the first generation is all a heterozygous red of a somewhat lighter shade than the original pure red strain as shown diagrammatically in Figure 40.

When plants of this heterozygous sort are crossed together, they yield plants producing red-kerneled and white-kerneled wheats in the proportion of sixty-three to one. The sixty-three kinds of red wheats are of

varying degrees of redness and may be classified after the manner of fluctuating variations with the greatest number of kinds at the intermediate degree between pure red and pure white. (See Figure 41.)

In order to test whether the sixty-four kinds of wheats produced in the second filial generation, as theoretically displayed in Figure 39, really contain separable, though indistinguishable, determiners for red-kernel, Nilsson-Ehle produced families of the third filial generation by self-crossing plants of the second generation. It was to be expected that, if these hybrid wheats of the second generation carried one, two, three, or more determiners for a red kernel as the theoretical tables in Figures 39 and 41 demand, their progeny would be distributed with reference to the number of red- and white-kerneled individuals, in the following ratios:—

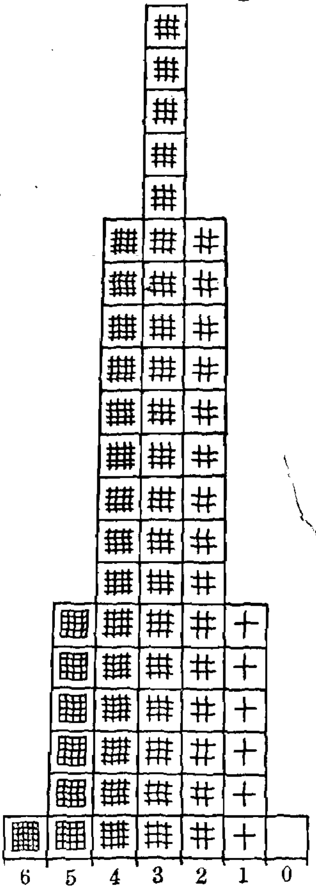


Fig. 41.—The distribution of the sixty-four possibilities in the F_2 generation when three similar determiners act together as a trihybrid.

3 red to 1 white when 1 heterozygous determiner for red is present.
15 red to 1 white when 2 } heterozygous determiners for red are present.
63 red to 1 white when 3 }
All red to no white when 4 or more }

Among seventy-eight sample families of the third generation inbred to test this theoretical conclusion, the actual results were:—

8 families giving the ratio of 3 red to 1 white.
15 families giving the ratio of 15 red to 1 white.
5 families giving the ratio of 63 red to 1 white.
50 families giving the ratio of all red to no white.

It has been actually demonstrated therefore, in the case of this particular strain of wheat: (1) that the factors producing red kernels are several in number; (2) that they act independently of each other in heredity; (3) that these several independent factors segregate; and (4) that any one red factor acting alone produces a "red" result.

The Nilsson-Ehle principle of cumulative determiners has been confirmed in America by East in a masterly series of breeding experiments upon maize.

In connection with the Nilsson-Ehle principle, it will be seen that the possible number of intergrades between the two extremes increases rapidly as the number of duplicate determiners increases. Thus with six duplicate determiners for the same character present, the ratio of possible dominants to recessives in the second filial generation would be 4095 to 1. The reappearance of this single recessive among 4095 domi-

nants would be extremely unlikely, and it might easily be mistaken for a mutation or a freak. Apparent blends of all intermediate degrees, however, would be sure to appear. Yet these are not blends in the "melting-pot" sense at all, but strictly cases of Mendelian dominance and segregation.

9. The Application of the Nilsson-Ehle Explanation to the Case of Rabbit Ear-length

The so-called blending rabbit ears, along with other similar cases, can now be made to fall into line, as pointed out by East and by Lang, with the Mendelian law of segregation.

If we assume that the long ear of the lop rabbit has only three independent but equal determiners for excess length, the case becomes one of Mendelian trihybridism with cumulative factors, which works out like Nilsson-Ehle's red-kerneled wheat in the following manner:—

In general the average for full lop ear-length may be placed at 220 mm. and for the ordinary short-eared rabbit [1] at 100 mm. The difference, or *the excess length of the lop ear*, is 120 mm., which, according to the trihybrid formula, corresponds to the six doses of the character symbolized in the upper left-hand square in Figure 39 by six large screw-heads, three coming from each parent respectively. If all of these independent determiners are equal as regards excess ear-length, each factor would represent an excess of 20 mm.

[1] Not the Belgian hare, as cited in the illustration given in Figure 36. The Belgian hare has typically a somewhat longer ear than the ordinary short-eared rabbit.

above the normal ear-length found in short-eared rabbits, that is,—

$$\frac{220 \text{ mm.} - 100 \text{ mm.}}{6} = 20 \text{ mm.}$$

When according to this computation a lop (20 mm. $\times$ 6 + 100 mm. = 220 mm.) and a pure short-eared rabbit (20 mm. $\times$ 0 + 100 mm. = 100 mm.) are crossed, if imperfect dominance occurs, which is a very common phenomenon, it is true that the offspring might present a "blended" appearance. If now these cross-breds of the first generation prove to be tri-hybrids with respect to excess ear-length, there would be sixty-four possibilities in their progeny segregating out just as in the red-kerneled wheat.

These possibilities would be arranged in the following frequencies:—

Number of Excess Ear-length Determiners	Number of Cases occurring out of 64	Total Length in Millimeters of Ears Resulting
6	1	220
5	6	200
4	15	180
3	20	160
2	15	140
1	6	120
0	1	100

Since the average litter among rabbits is about five, the chances that these five rabbits will breed true to their hybrid parents and form a perfect blend between their grandparents is 20 out of 64, while the chance of their being like either grandparent is only one out of 64.

It should be noted further that 50 out of 64, or 77 per cent, of these hybrids of the second filial generation would have an ear-length between 140 and 180, thus approximating a "blend" closely enough to be so classified upon a casual inspection.

If it should be found, moreover, that excessive ear-length in rabbits is due to more than three duplicate determiners, the possibilities of getting anything but an apparent blend would be much decreased.

Furthermore, the fact that the fractional ear-lengths of the hybrid rabbits in Castle's experiments bred approximately true in the second and subsequent filial generations, may also be explained by the Nilsson-Ehle hypothesis.

For example, half lop lengths, according to this explanation, are those with three doses of the determiner for excess ear-length. It follows that the progeny of two rabbits each carrying three doses of a determiner will likewise, after the reduction during the maturation of the germ-cells, have three doses of the determiner $\left(\frac{3+3}{2}=3\right)$.

It would be interesting to breed rabbits having ears of one-eighth lop length in which, according to the foregoing hypothesis, there presumably would be present only a single determiner for excess ear-length, with ordinary short-eared rabbits having no excess ear-length, in order to see if the expected Mendelian three-to-one proportion for a monohybrid would appear in the progeny.

10. Human Skin Color

Finally, in man the skin-color of mulattoes, in hybrids between blacks and whites, has often been mentioned as a case of blending inheritance since mulattoes are commonly supposed to produce mulattoes when they mate together or a blending degree of color when they mate with some one whose shade of color is unlike their own.

This matter has been carefully and extensively studied by Davenport and Danielson [1] who came to the conclusion that the pure-blooded negro of the West Coast of Africa possesses two pairs of duplicate genes for black pigmentation (*AABB*) which, though separately heritable, are cumulative in effect. The corresponding formula for black pigmentation in a normal white is *aabb*. When black (*AABB*) and white (*aabb*) are crossed, the formula for the mulatto will be *AaBb* in which half the total amount of black pigment of both parents is present.

The result of crossing two mulattoes is shown by checkerboard diagram in Fig. 42.

The figures in the corners of the squares indicate the total amount of black pigment in each case upon the supposition that $A = 19$, $B = 16$, $a = 2$ and $b = 1$, these values being determined by the color-top method described by Davenport and Danielson.

In the table on page 191 is a classification of these possibilities according to the amount of black pigment

[1] Heredity of Skin Color in Negro and White Crosses. Pub. No. 188 of the Carnegie Inst. of Washington.

present, and in Figure 43 is a graphic representation of the numerical chances for skin-color in spite of segregation when two mulattoes mate.

	AB	*Ab*	*aB*	*ab*
AB	*AB* *AB* 70	*Ab* *AB* 55	*aB* *AB* 53	*ab* *AB* 38
Ab	*AB* *Ab* 55	*Ab* *Ab* 40	*aB* *Ab* 38	*ab* *Ab* 23
aB	*AB* *aB* 53	*Ab* *aB* 38	*aB* *aB* 36	*ab* *aB* 21
ab	*AB* *ab* 38	*Ab* *ab* 23	*aB* *ab* 21	*ab* *ab* 6

FIG. 42.—Checkerboard to show the different expected shades of black color in the possible offspring of two mulattoes. A = 18; B = 17; a = 2; b = 1 percent of black pigment. Data from Davenport and Danielson.

The case thus is similar to that of Nilsson-Ehle's brown-chaffed wheat already described, so that the possible range of offspring of a mulatto pair is all the way from black to white. Theoretically, any one of five degrees of pigmentation, including the extremes of black and white, may be expected. The chances

A Classification of Hybrid Skin Colors on the Basis of the Factor Hypothesis

Genes	Gametic Formula	Color	Relative Frequency	Range of Percent of Pigment in Offspring	Popular Names (Jamaica)
All absent	aabb	White	1:16	0–11	Pass-for-white Mustifino Mustifee Octaroon
One present	Aabb aaBb	Light	4:16	12–25	Quadroon
Two present	AAbb AaBb aaBB	Medium	6:16	26–40	Mulatto
Three present	AABb AaBB	Dark	4:16	41–55	Mangro Sambo
All four present	AABB	Black	1:16	56–78	Negro

which any one of these five degrees of color has of reappearing in a child of mulatto parents is indicated in Fig. 43. It is evident that there is more likelihood, in point of fact six chances out of sixteen, that a child from mulatto parents will be mulatto than anything else, and this expectation ordinarily agrees with the realization, but there are four chances out of sixteen that it will be either darker or lighter than its parents and one chance out of sixteen that it will be as dark or as light as its black or white grandparents.

Davenport and Danielson show several illuminating photographs of large families of children from mulatto parents in which a manifest inequality of color shade among the different children is apparent as would be expected according to this explanation.

Blending inheritance, then, is probably nothing more

than Mendelian alternative inheritance in which two or more similar genes, duplicate or cumulative, are concerned. One explanation instead of two or three,

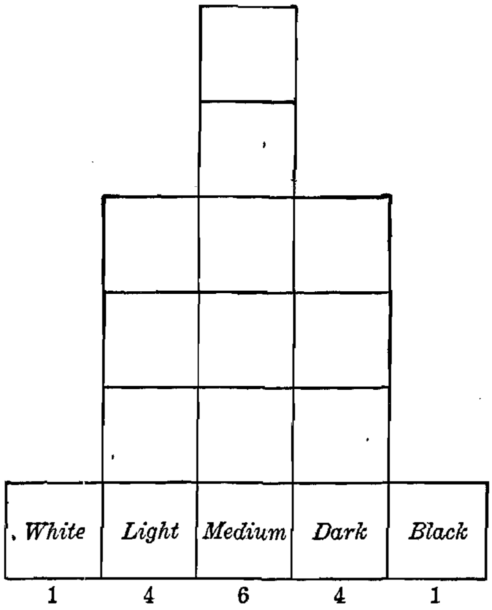


FIG. 43.—Diagram to show the expectation of color and its frequency in the cross between two mulattoes.

therefore, is sufficient to dispose of an array of apparently diverse phenomena.

"We may therefore conclude," says Conklin, "that the Mendelian law of heredity, especially as regards segregation of inheritance factors, is of universal occurrence—that there is no other type of inheritance."

CHAPTER IX

OLD TYPES AND NEW

1. The Distinction between Reversion and Atavism

There are two ways in which types of animals or plants that are different from the present ones may be conceived to arise, namely, by the reappearance of old types and by the formation of new ones. In the reappearance of old types a distinction may be drawn between reversion and what has been termed atavism.

Atavism, or "grandparentism," may be defined as skipping a generation with the result that a particular character in the offspring is unlike the corresponding character in either parent, but instead, resembles the character in one of the grandparents.

In *reversion*, on the contrary, a character reappears which has not been manifest perhaps for many generations, although it was actually present in some remote ancestor. J. Arthur Thomson's definition of reversion is: "All cases where through inheritance there reappears in an individual some character which was not expressed in his immediate lineage, but which had occurred in a remoter, but not hypothetical, ancestor."

This distinction between atavism and reversion becomes clearer by illustration.

If heterozygous brown-eyed individuals mate, there is one possibility in four that their offspring will have blue eyes unlike their own, but like the two blue-eyed

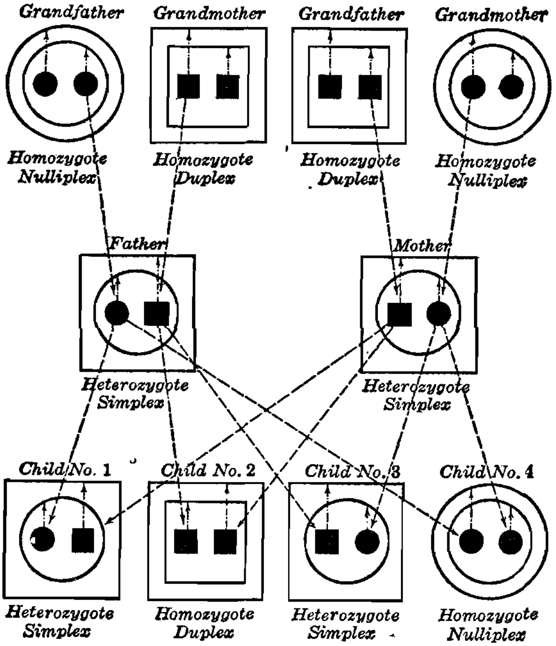


FIG. 44.—Three generations of a Mendelian monohybrid. The outlines represent the somatoplasms with the phenotypic character on the outside. The black symbols inclosed within the somatoplasm stand for the germplasm in the form of gametes. The short dotted arrows indicate the relation between germplasm and somatoplasm. The long dotted arrows indicate possible recombinations of germplasms.

grandparents. Such a blue-eyed child would be an instance of atavism. The explanation of this apparently inconsistent hereditary behavior is perfectly simple in the light of the Mendelian ratios, as shown

diagrammatically in Figure 44, in which the circles represent the blue-eyed and the squares the brown-eyed character.

This figure also illustrates what typically occurs in the formation of Mendelian monohybrids of the first and second filial generations. The squares are symbols for the *dominant* characters, while the circles are symbols for the *recessive* characters. When the two are superimposed, the circle recedes from view. The large outside figures indicate the *somatoplasm*, therefore the *phenotype*. The small inclosed figures indicate the *germplasm*, therefore the *genotype*. The short dotted arrows indicate what it is that determines the somatoplasm in each case, while the long dotted arrows show what possible recombinations of germplasms can be made. Child No. 4 is an "extracted recessive" derived from dominant parents, but with one recessive grandparent on each side. It is a case of "atavism," or taking after the grandparent. Notice that atavism can occur only by alternative inheritance.

To quote Davenport: "In the majority of cases atavism is a simple reappearance in one fourth of the offspring of the absence of a character due to the simplex nature of the character in both parents."

An illustration of *reversion* would be the reappearance of the ancestral jungle-fowl pattern in domestic poultry or of the slaty blue color of the ancestral rock-pigeon among buff and white domestic pigeons, for the ancestral character or characters in this type of hereditary behavior, as said before, reappear only after a lapse of many generations.

2. FALSE REVERSION

"Around the term 'reversion,'" Bateson observes, "a singular set of false ideas have gathered themselves." In proof of this statement there may be cited at least five categories of apparent reversion which properly ought not to be classed as true reversion.

A. ARRESTED DEVELOPMENT

Feeble-mindedness is not reversion to ancestral forms of less intelligence, but an instance of *arrested development* when, for some reason, the individual fails to accomplish his normal cycle of development.

Likewise harelip in man is not a case of reversion to rabbit-like ancestors in which harelip is the normal condition, but it is ordinarily due to an arrest or failure of certain embryonic steps essential to the development of the usual form of human lip.

B. VESTIGIAL STRUCTURES

These are the vanishing remains of characters that were formerly of significance. They do not represent something latent that is now *re*appearing, for they have never yet disappeared phylogenetically, and consequently they cannot be regarded as true reversions.

The muscles under the scalp which enable those persons possessing them to wiggle the ears; the palatine ridges in the roof of the mouth of many babies and some adults which resemble the ridges in the roof of a cat's mouth; the vermiform appendix, a necessary

part of the digestive apparatus of many animals but fraught so often with evil consequences to man; these and scores of similar characters, which, taken together, make man in the eyes of the comparative anatomist a veritable old curiosity shop of ancestral relics, are the last traces of characters which formerly had a significance in some of man's forbears. Having lost their usefulness, these structures still hang on to the anatomical household as pensioners. They have not been recalled from the past, but have always been with us, although of diminishing importance. In no sense, therefore, can they be called reversions.

C. ACQUIRED CHARACTERS RESEMBLING ANCESTRAL ONES

Sometimes the drunken descendant of a drunken great-grandparent has acquired this characteristic through his own initiative quite aside from any ancestral contribution to his germplasm. This is not reversion, but reacquisition resembling the ancestral condition.

Again, tame animals that run wild acquire habits resembling those of their wild ancestors, but this is not necessarily reversion. It is the natural response of feral animals to the conditions of wild life.

D. CONVERGENT VARIATION

The European hedgehog, *Erinaceus*, an insectivore, the American porcupine, *Erithizon*, a rodent, and the Australian spiny anteater, *Echidna*, a monotreme, are all mammals which have developed in a similar manner

the very peculiar device of dermal spines. There is no reason, however, for regarding this character as due to descent from a common spiny ancestor. It is not reversion to an ancestral type, but rather a case of convergent variation. Similarity does not always indicate genetic continuity.

In the case of birds albinism, melanism and flavism are modifications of ordinary pigmentation which appear irregularly among many different species as pathological "sports," but no one of these conditions can be regarded as reversions to ancestral white, black, or yellow types.

E. REGRESSION

Galton's "law of regression" refers to the widespread phenomenon already explained of a constant swinging back to mediocrity which the breeder must oppose with continual selection in order to maintain the standard of any particular strain. We have seen that within a "pure line," regression is complete and that in populations made up of a mixture of pure lines it is a factor that must invariably be considered. Regression, however, has to do with fluctuating variations and does not bring about a permanent change of type. It should, therefore, not be confused with reversion.

3. Explanation of Reversion

Darwin, who did not always differentiate between reversion and atavism, suggested that reversion was due sometimes to the action of a more natural en-

vironment, as in the case of animals set free after having been in captivity, and sometimes to hybridization, since there seems to be a general tendency of hybridized organisms to "revert" to ancestral types.

It is now known that reversion, like atavism, is simply a case of latent characters becoming apparent according to the Mendelian principle of segregation. To quote Davenport: "There is nothing more mysterious about reversion, from the modern standpoint, than about forming a word from the proper combination of letters."

4. The Art and Science of Breeding

The *art* of breeding animals and plants has been practiced from very early times while the *science* of maintaining old types and initiating new ones is of comparatively recent origin.

Some of the methods that have been employed with varying degrees of success are:—

A. Mass selection;
B. Pedigree breeding;
C. Inbreeding;
D. Hybridization;
E. Genotypic selection.

A. MASS SELECTION

The natural thing to do in the maintenance or improvement of cultivated plants and domestic animals is to select seeds from the best looking plants and to

breed together from the flock or herd those animals which appear most desirable. This has been the method from the beginning and there is a reason for the considerable degree of success that has followed this obvious mode of procedure. The method, however, has its limitations because it is *entirely phenotypic* and the breeder is sure to find with Dryden that "all as they say that glitters is not gold."

Two methods of mass selection, as applied to plants, may be mentioned that differ in the extent to which the environment is recognized as a contributing factor.

a. The Method of Hallet

The English wheat-grower Hallet formulated this method in 1869 and it has been in common use for a long time. It consists in placing the organisms to be bred in the very best possible environment and then choosing those individuals making the best showing as the stock from which to breed further, a procedure based upon the deep-seated belief that acquired characters are inherited.

For example, in a field of wheat, plants near the edge of the field which, from lack of crowding or by reason of proximity to an extra local supply of fertilizer or any other favorable environmental factor, make a more vigorous growth than their neighbors, are selected in the hope that the gains made by them will be maintained in their offspring.

We have seen that it is very questionable whether acquired characters due to environmental conditions

play any rôle whatever in heredity. The phenotypic character does not always indicate what the germplasm will subsequently do, and when the true genotypic constitution of the germplasm is still further masked by the temporary fluctuations caused by a modified environment it is increasingly difficult to select wisely from the display of variants those which will produce the best ancestors for the future stock.

That this common procedure of selecting the best-appearing animal in the flock and the biggest ear of corn in the bin has met with a large degree of success in the past is due entirely to the fact that in many instances the phenotypic character is an actual expression of the genotypic constitution. This is not always the case, however, and we cannot now fail to see that the method is blind and full of error. Its successes are due to the indirect results of chance rather than to a direct control of the factors of heredity.

b. *The Method of Rimpau*

Contrasted with the method of Hallet of augmenting acquired characters and then selecting from them the best display, is the method of Rimpau, who experimented for two decades with various grains and, finally, among other results, produced the famous Schlandstedt barley.

Rimpau's method is to sow grain under ordinary conditions with a minimum rather than a maximum amount of fertilizer and then to select individuals, neither from the rich spots nor from the edges of the

field where there is little crowding, but from situations where the environmental conditions are ordinary or even unfavorable. Individuals making a good showing under such usual, or even adverse, conditions are worthy by *nature* rather than by *nurture* and are consequently most desirable as progenitors of future stock. By this method the attempt is not to keep the progeny of single individuals separate, but to mass together the best as they appear under ordinary normal environment.

This again is an indirect method of procedure, although the character of the germplasm is more nearly hit upon in this way than by Hallet's method, since the mask of temporary accessory modifications is stripped so far as possible from the somatoplasm, and the phenotype made to approximate the genotypical constitution.

B. PEDIGREE BREEDING

Mass selection, or the choosing of a number of individuals out of a population to be the progenitors of the next generation, is subject to repeated backsliding to mediocrity and consequently the selection must be made over and over again in each generation. A greater degree of success than is possible by this method has followed attempts to isolate single self-fertilizing individuals that manifest the desired qualities and to establish pedigrees from this isolated stock. This is Johannsen's method of the pure line and is particularly applicable to self-fertilizing plants, al-

though it may be extended to clones, parthenogenetic lines and to homozygous crosses.

A quotation from the memoirs of the Manchu emperor K'ang-Hsi, 1662-1723, translated from *L'Empire Chinois*, E. R. Huc, will illustrate an early application of the pedigree method. "On the first day of the sixth moon I was walking in some fields where rice had been sown to be ready for the harvest in the ninth moon. I observed by chance a stalk of rice already in ear. It was higher than all the rest and ripe enough to be gathered. I ordered it brought to me. The grain was very fine and well grown, which gave me the idea to keep it for a trial and see if the following year it would preserve its precocity. It did so. All the stalks which came from it showed ear before the usual time and were ripe in the sixth moon. Each year has multiplied the produce of the preceding, and for thirty years it is the rice which has been served at my table. It is the only sort which can ripen north of the great wall, where the winter ends late and begins very early; but in the southern provinces, where the climate is milder and the land more fertile, two harvests a year may be easily obtained, *and it is for me a sweet reflection to have procured this advantage for my people.*"

In the last century the isolation of pure lines was practiced notably by the Englishman LeCoutour, who isolated 150 varieties of wheat and by the Scotchman Shirreff, who worked with various cereals.

In recent years the principle has been extensively applied with remarkable results, particularly by

Nilsson of Svalöf in Sweden, upon peas, potatoes, clovers, grasses and grains.

Among others in America, Hays has isolated pedigrees of wheat at the Minnesota Agricultural Experiment Station, which within a decade have been grown on thousands of acres and have "made possible the increased production of wheat throughout the northern States and Canada."

An isolation method that has been successfully applied to the sugar-beet industry is that of Vilmorin. The seeds from each plant to be tested are sown in separate beds from which upon maturity samples are taken and tested for sugar content. The plants from the bed furnishing the sample containing the highest percentage of sugar are then used as the seed producers for the next generation. In this way by continual selection an improved strain is maintained.

C. INBREEDING

When breeding is kept up between individuals of the same stock it tends to perpetuate or preserve the distinctive characteristics of that stock, a practice that was advocated in the Mosaic law,—"Thou shalt not let thy cattle gender with a diverse kind; thou shalt not sow thy field with mingled seed." (Levit. XIX:19.)

Numerous experiments to test the effect of inbreeding have been carried out upon various organisms.

Darwin, for instance, planted morning-glories, *Ipomœa*, derived from the same stock of seeds, in two

beds which were laid out side by side, that is, in an environment as nearly the same as possible, but with half of the beds screened from insects which usually transfer pollen from flower to flower. In the screened half where all insects were excluded the flowers were of necessity self-fertilized, while in the exposed half they were presumably cross-pollinated by insects which had free access to them. The seeds produced in the two beds were kept separate and the experiment was continued for ten years, so that at the end of that time two lots of morning-glories, one self-fertilized for ten generations and the other presumably cross-pollinated for the same length of time, were obtained for comparison. The criterion Darwin used was the vigor of the plants as shown by the length of the vine. He found that the cross-pollinated plants were to the self-pollinated ones as 100 to 53, and his conclusion was, consequently, that cross-pollination is beneficial and self-pollination is detrimental.

Ritzema-Bos inbred rats for twenty generations. For the first ten generations the average number of young per litter was 7.5, while for the last ten generations it fell to 3.2.

Weismann inbred mice for twenty-nine generations and obtained a parallel result. For the first ten generations the average number per litter was 6.1, for the second ten generations 5.6, and for the last nine generations 4.2.

Dr. Helen King, on the other hand, practiced close inbreeding with white rats for 40 generations comprising over 20,000 individuals obtained by mating

brothers and sisters from the same litter at the end of which time the animals were larger and more vigorous than those not inbred.

Shull found in growing Indian corn that loss of vigor results from continual self-fertilization, and many breeders have had similar experiences with animals as well as other plants.

In the case of the pomace fly, *Drosophila*, Castle inbred brother and sister for fifty-nine generations without diminishing the fertility of the line.

Hornaday cites the case of the deer in the royal herd at Windsor which arose from one male and two females introduced from New Zealand in 1862. The herd now numbers 20,000 and shows no signs of deterioration.

No arbitrary law with respect to the effects of inbreeding upon vigor and fertility can be laid down, therefore, which will apply equally to all cases.

Nature has secured, often by elaborate devices, a separation of the sexes, especially among the higher organisms, and in consequence there has arisen an unavoidable necessity of outcrossing. The intricate adaptations existing between insects and flowers, for example, seem to be directed entirely toward insuring outcrossing among plants.

There are, on the other hand, various well known provisions in nature to insure inbreeding. The majority of plants are probably self-fertilized while hermaphroditic animals, which sometimes at least are self-fertilized particularly among the lower forms, are very common.

The whole matter of inbreeding and the part it plays in emphasizing defects has received a fresh interpretation in the light of Mendelism.

There is a widespread popular belief that inbreeding is injurious and that it is necessary to outcross in order to maintain the vigor and avoid the defects of any line, but inbreeding in itself may not necessarily be injurious. The consequence of inbreeding as shown by the working of Mendelian laws is that latent or recessive characters tend to become homozygous and so brought to the surface, while outcrossing brings about the formation of heterozygous traits which mask recessive characters and render them ineffective.

In the case of mankind, consanguineous marriage of various degrees has long been forbidden by law or custom in many races, particularly among the Jews, Mohammedans, Indians and Romans. On the other hand, the Persians, Greeks, Phœnicians and Arabs have freely practised inbreeding, while one of the longest of known human pedigrees, a royal line of Egypt, is notorious for close inbreeding, even to the mating of brother and sister.

There has been a greater degree of inbreeding in the Puritan stock of New England than is commonly realized. David Starr Jordan points out that a child of to-day, supposing no inbreeding of relatives had occurred, would have had in the time of William the Conqueror, thirty generations ago, 8,598,094,592 living ancestors. If this theoretical supposition were really so, it would seem quite possible for every New Englander to-day to have at least one ancestral representative who won glory under William.

The difference between the unthinkable number given above and the actual number of probable ancestors alive thirty generations ago emphasizes the fact that inbreeding must have occurred freely.

Cousin-marriages, although producing a high percentage of defects, do not necessarily produce undesirable traits. They simply bring out latent or recessive characters for the reason that under these conditions defect meets defect instead of the opposite normal condition which would dominate the defect and cause it not to appear.

Since a recessive trait may be properly regarded as the *absence* of a positive dominant character, it more frequently stands for an undesirable feature than otherwise. Thus it comes about that inbreeding, by combining negative features, may "produce" a defective strain.

Outcrossing always increases heterozygous combinations in the germplasm and covers up undesirable recessive traits through the introduction of additional dominant traits. Inbreeding, on the contrary, tends to simplify the germplasm, that is, to make it more homozygous, and so to bring recessive defects to the surface.

D. HYBRIDIZATION

Among the first to use the powerful tool of hybridization were Koelreuter, 1733-1806, in Germany, and Knight, 1758-1838, in England. These pioneer transgressors of the Mosaic law cited in the foregoing paragraph, opened up a broad road to the army of the Mendelians who were to follow them. Not only have

individuals of two varieties showing hereditary differences been hybridized but successful crosses have been artificially brought about between individuals belonging to different species, to different genera and even to different groups still more distantly related to each other.

It may be possible to point out at least two general methods of utilizing hybridization.

a. The Method of Burbank

This is a method of greatly increasing the number of variants by promiscuous hybridization and then of eliminating all except those of a desired phenotypic combination. Indirectly it depends upon the principle of the segregation of unit characters which makes possible *rearrangements* of these characters according to the laws of chance. The characters themselves remain unchanged, since nothing new is produced by hybridization except *new arrangements* of existing characters.

The spectacular success of Luther Burbank in "creating" new plant forms is due largely to his very extensive hybridizations, his skill in detecting among the varying progeny the winning phenotype and his ruthless elimination of the great majority of variations that do not quite fill his requirement.

The successful combinations must be propagated in most instances asexually by grafting, cuttings, bulbs, etc., rather than sexually through the medium of seeds, because new genotypes which will breed true are

not necessarily isolated by this procedure. The consequence is that Burbank's method cannot be utilized in animal breeding to any great extent where the maintenance of a desirable strain by asexual propagation is out of the question.

It will be seen that this method is fortuitous and to a certain extent unscientific in that no one can repeat the exact conditions of the experiment and arrive at the same results. It depends upon the chance mixing up of a large number of possibilities and then in not being distracted or blinded by the *good* while selecting the *best*. In the hands of a skilful plant breeder with unlimited resources at his command it may result in much practical achievement, but it does not particularly illuminate the path of other breeders who wish to repeat the experiment. It is after all a selection of phenotypes and, therefore, forever open to error, since phenotypes do not always indicate what the behavior of their constituent genotypes will be in heredity.

b. The Method of Mendel

The method of Mendel, like the foregoing, depends upon hybridization with the difference that the desired combination is sought directly by definite predetermined crosses, according to the expectations of the Mendelian ratios, rather than through the random result of fortuitous combinations. It is a method which has been rendered possible by the determination of Mendel's laws of dominance, and of the independence and segregation of unit characters which give to the experimental

breeder definite expectations and a method of procedure.

If, upon hybridization, the desired character behaves like a *recessive,* then all that is necessary to establish a pure stock exhibiting the character in question, is to breed two recessives together, because recessives are always homozygous and, regardless of their ancestry, breed true.

On the other hand, if the desired character proves to be a *dominant,* then it is necessary to determine whether it is present in a duplex or a simplex condition; in other words, whether it is homozygous or heterozygous, for only homozygous organisms breed true. Establishing a strain consists, consequently, in making an organism homozygous.

The test to determine whether a dominant character is homozygous or heterozygous, that is, whether it will breed true or not, can be made by a single cross according to the procedure outlined in paragraph 8 of Chapter V. If, upon crossing the individual to be tested with a recessive, it produces an entirely dominant progeny, then its germplasm is duplex for this character, and it will always reproduce the character in either duplex or simplex condition according to whatever cross may be made with it. When crossed, for instance, with another duplex dominant like itself, a pure homozygous strain of the character in question will be perpetuated.

If, on the contrary, the dominant character to be tested proves to be simplex or heterozygous, as determined by the fact that, when crossed with a recessive, 50 per cent of the progeny are recessive, then

it requires more than a single generation to establish a homozygous dominant strain.

In random inbreeding of diverse strains *if the recessives are constantly eliminated as they appear*, a population is gradually obtained which is composed of an increasing number of dominants so that after only a few generations the chances are much reduced that recessives will again appear, which means the practical purity of the strain.

E. GENOTYPIC SELECTION

The success, however, of any method of originating new types of organisms or of improving old ones must depend in the long run upon the selection of germinal differences.

The difficulty here of course lies in the fact, that we may only know the potential germplasm from its performance in producing somatoplasm, but Mendelism with its analysis of the genes through breeding, certainly has gone a long way toward making genotypic selection possible and definite. Moreover, the preservation and exploitation of mutations when they are known is certainly along the line of genotypic selection, since mutations when isolated may become the progenitors of desirable new lines. Accordingly until the secret of the origin of mutations is solved the work of the successful breeder consists to a very large extent in simply taking what mutations nature spontaneously furnishes to him rather than in attempting to force nature into producing something new.

5. Heterosis

When hybrids are formed the first hybrid generation not only shows more variability but also more vigor than the parental strains and this vigor is in proportion to the number of factors in which the parents differ, because in hybridization there is a pooling of hereditary resources. Such hybrid vigor is termed *heterosis.*

East and Hayes describe, for example, a cross between two different wild varieties of tobacco in which the average height of over fifty plants of each of the two wild parents was 31 and 54 inches respectively. Of an equal number of hybrids of the first generation the average height was over 67 inches under the same environmental conditions. Shull and East, working separately upon maize, came to the same conclusion, namely, that the first hybrid generation following an artificial cross is decidedly more vigorous than the parental stocks from which it is derived. This is shown in Figures 45 and 46.

The mule is a notorious hybrid that possesses more "kick" than its parents.

FIGS. 45 and 46.- Results of crossing two inbred strains of corn. At the left in Fig. 45 are two inbred varieties. The tall corn at the right is the result of crossing them. In Fig. 46, the basket at the right represents the average production of two inbred strains after three generations of inbreeding—61 bushels per acre. The basket at the left shows the first generation results from crossing them—101 bushels per acre. After East and Hayes.

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CHAPTER X

THE CARRIERS OF THE HERITAGE

1. Introduction

Heredity, as has been shown in the introductory chapter, is essentially a matter of continuity between succeeding generations of living organisms. This continuity may be direct, as when a mother protozoan divides into two daughters, or it may be indirect, as illustrated by the relationship of a father and son, an uncle and nephew, or any other relatives of varying degrees of kinship which, taken singly or collectively, are somatoplasms derived from a common stream of germplasm.

It is the purpose of the present chapter to consider this material continuity between succeeding generations and to discover, if possible, just what are the carriers of the heritage from one generation to another. To this end it will be necessary in the first place to take up what is meant by the "cell theory."

2. The Cell Theory

In 1838-1839 the "cell theory" of Schleiden and Schwann, which affirms that all organisms, both plant and animal, are made up of cellular units, had its birth.

Robert Hooke, as early as 1665, had described "little boxes or cells distinguished from one another" which he saw in thin slices of cork, and to him is due the rather unfortunate use of the term "cell" which has survived in biological writings to this day. The reason this term is unfortunate is because walls, which are ordinarily the characteristic feature of any cell, such as a prison cell, are usually the least important part of the structure of a living cell, often indeed being entirely absent.

3. A Typical Cell

A typical undifferentiated cell is represented diagrammatically in Figure 47. Near the center of the

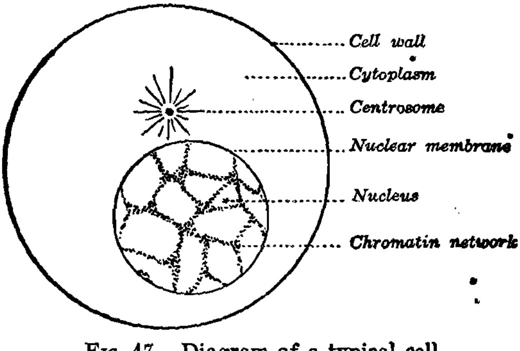

Fig. 47.—Diagram of a typical cell.

cell the *nucleus* is shown surrounded by a *nuclear membrane.* The nucleus, in common with the enveloping *cytoplasm,* is made up of living substance called *protoplasm* (Hugo von Mohl, 1846), and around the whole there is usually formed a *wall* or membrane which

serves to separate one cell from another. Within the protoplasm there may be a considerable amount of non-living substance in the form of salts, pigments, oil-drops, water, and other inclusions of various kinds.

The nucleus is to be regarded as the headquarters of the whole cell, since changes which the cell undergoes seem to be initiated in it, while cells deprived of their nuclei cannot long survive. A single instance will serve to show the vital part which the nucleus plays in the life-history of the cell. In 1883, Gruber found that after rocking a thin cover-glass back and forth in a drop of water containing a collection of the protozoan *Stentor*, which has a long chain-like nucleus, these tiny animals could thus be cut into fragments, which would in some instances recover from the operation and regenerate into complete individuals. Only those pieces, however, which contained a fragment of the nucleus regenerated into new Stentors, while pieces of relatively large size which lacked a fragment of nuclear substance very soon disintegrated.

The nucleus, it should be said, is made up of more than one substance, a fact that is easily demonstrated by processes of staining, in which certain dyes, through chemical union, stain a part but not the whole of the nuclear substance. The part most easily stained is called *chromatin*, that is "colored material," and during certain phases of cell life the chromatin masses together within the nucleus into visibly definite structures or bodies termed *chromosomes.*

Throughout all the various cells that make up the individuals of any one species these chromosomes ap-

pear to be practically constant in number with some exceptions to be mentioned later in connection with sex. This law of the constant chomosome number for any species was first stated by Boveri in 1900.

The chromosomes of different organisms vary in number from two in the worm *Ascaris* up to perhaps 1600, according to Haecker ('09), in certain radiolaria. A recent list records the number of chromosomes typical for 960 different animals.[1] Species which apparently are closely related may differ widely with respect to the number of their chromosomes, while species of unquestionably remote relationship may have an identical number of chromosomes in each of their cells. The number of chromosomes characteristic for a species, therefore, is in no way an index to the complexity or degree of differentiation of the species.

Besides the nucleus there may often be identified in the cytoplasm of the animal cell a tiny body known as the *centrosome.* At certain times in the life-cycle of a cell the centrosome becomes the focal point of peculiar radiating lines, which play an important part in the behavior of the cell, particularly during the period of division.

Every cell passes through a cycle of life which may be compared with that common to individuals. It is born from another cell; passes through a vigorous youth characterized by growth and transformation; attains maturity when the metamorphoses of its earlier life give place to a considerable degree of stability; and finally, after a more or less extended period of normal

[1] *Jour. of Morphology,* vol. 34, pp. 1-67, 1920.

activity reaches old age, and death completes the cycle. In most instances, however, before this final phase is reached, the cell gives place to daughter-cells through fission, after the manner of most protozoans, and a new cell cycle is begun.

Sometimes the road of differentiation has been traveled so far that it is apparently impossible, as in the case of the complicated brain-cells, to retrace these steps of differentiation and begin again. In such instances the outfit of cells provided in the embryo determines the numerical limit of the cells available throughout life. When this supply is exhausted no more cells appear to replace those which have been worn out.

4. Mitosis

The ordinary process by which two cells are made out of one is termed *mitosis.* It occurs constantly, and particularly during growth, in all cellular organisms. A series of diagrams, modified from Boveri, illustrating the typical phases of mitosis is given in Figures 48 to 57.

The resting cell (Fig. 48) is characterized by the presence of a nuclear membrane, a single centrosome, and by a chromatin network within the nucleus. In the *beginning of the prophase* (Fig. 49) the centrosome has divided into two parts, while in the *early prophase* (Fig. 50) the two centrosomes have moved farther apart and definite separate chromosomes have formed out of the chromatin network. The *prophase proper* (Fig. 51) is marked by the vanishing of the nuclear

membrane and the more compact form of the chromosomes. At the *end of the prophase* (Fig 52) the chromosomes have come to lie at the equator of the cell,

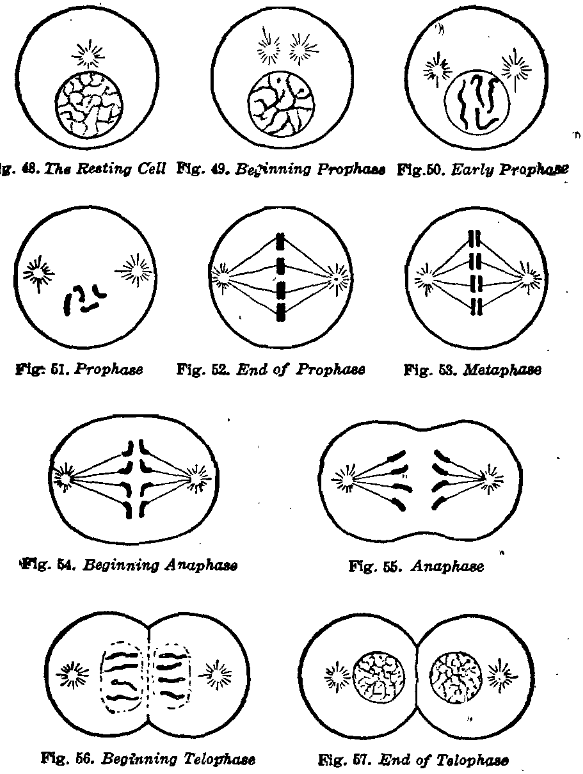

Fig. 48. *The Resting Cell* Fig. 49. *Beginning Prophase* Fig. 50. *Early Prophase*

Fig. 51. *Prophase* Fig. 52. *End of Prophase* Fig. 53. *Metaphase*

Fig. 54. *Beginning Anaphase* Fig. 55. *Anaphase*

Fig. 56. *Beginning Telophase* Fig. 57. *End of Telophase*

FIGS. 48–57.—Diagrams illustrating mitosis. After Boveri.

being connected by the mantle fibers with the centrosomes, each of which now occupies a polar position. In the *metaphase* (Fig. 53) the chromosomes split lengthwise, and at the *beginning of the anaphase* (Fig.

54) these half-chromosomes commence to separate from each other and to move toward the poles, while the mantle fibers shorten. During the *anaphase* (Fig. 55) the cell body lengthens and begins to divide, while the migration of the half-chromosomes toward the poles is completed. In the *beginning of the telophase* (Fig. 56) the half-chromosomes grow until they attain full size and the division of the cell body into two parts becomes complete. The mantle fibers have disappeared and the nuclear membrane begins to reform around the chromosomes. Finally, at the *end of the telophase* (Fig. 57) the nuclear membrane becomes complete, the chromosomes break up into a chromatin network, and two resting cells take the place of the single one with which the process began (Fig. 48).

5. Sexual Reproduction

The mechanism by means of which two cells unite to make one in sexual reproduction is quite as complicated as that of mitosis by which one cell is transformed into two.

In sexual reproduction there are two kinds of germ-cells, the egg and the spermatozoan respectively, which take part in producing a new organism. These cells are structurally unlike each other in nearly every particular, but each is a true cell, which von Kölliker made clear as early as 1841, and each has typically the same number of chromosomes in its nucleus, a fact more recently determined by van Beneden in 1883.

The egg-cell is often supplied with one or more

envelopes of protective or nutritive function, and it is usually distended with stored up yolk, in consequence of which it is comparatively large and stationary. The result is that whatever locomotion is necessary to bring the two cells together for union devolves upon the sperm-cell. Consequently the sperm-cells are practically modified into nuclei with locomotor tails of cytoplasm, and frequently, in addition, with some structural modification for boring a way into the egg-cell. They are, moreover, much more numerous than the egg-cells, so that although many go astray, never fulfilling their mission, the chances are nevertheless good that some one of them will reach the egg and effect fertilization.

Ordinarily only one sperm enters the egg, but when several succeed in penetrating into the egg-cytoplasm only one proceeds to combine with the egg nucleus, that is, only one sperm nucleus is normally concerned in the essential process of fertilization.

It was formerly thought by the school of "ovists" that in fertilization the essential process is a stimulation of the all important egg by the sperm. The opposing school of "spermists," on the other hand, regarded the egg simply as a nutritive cell the function of which is to harbor the all important sperm. It is now known that both the egg- and the sperm-cell are equally concerned in fertilization, which consists in the union of their respective nuclei within the cytoplasm of the egg.

6. Maturation

Certain preliminary changes of a preparatory nature, termed *maturation*, regularly precede the union of the nuclei of the two sex-cells in fertilization.

These maturing changes result in reducing the outfit of chromosomes in each sex-cell to one-half the original number, a process which is necessary in order to maintain the chromosomal count which is characteristic for any particular species and which is known to exist unbroken from generation to generation. If there were no such reduction, then the fertilized egg, formed by the union of egg and sperm nuclei, would contain double the characteristic number of chromosomes, and during the formation of a new individual, the number in all the cells arising by mitosis from such a fertilized egg would likewise be double. When the germ-cells of such individuals unite in fertilization, the original number of chromosomes would be quadrupled, and so on in geometric progression throughout subsequent generations. In 1883, too late for Darwin to learn of it, van Beneden discovered the important fact that the mature germ-cells, as expected, actually contain only half the normal number of chromosomes.

The mature egg- or sperm-cell, with half its normal number of chromosomes, is termed a *gamete* (marrying cell), while the fertilized egg which is formed by the union of two gametes (mature egg- and sperm-cell), and which consequently has the characteristic number of chromosomes, is called a *zygote* (yoked cell).

A diagrammatic representation of the process of

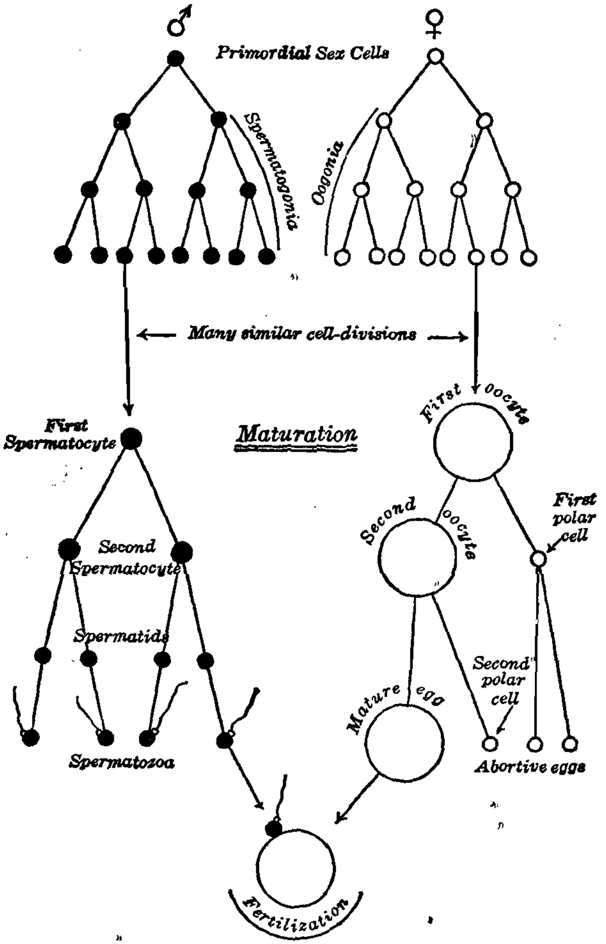

Fig. 58.—Diagram to show typical maturation and fertilization.

maturation is shown in Figure 58. The number of chromosomes (not shown in the diagram) remains con-

stant in each germ-cell respectively until the division of second spermatocytes into spermatids which are subsequently transformed into spermatozoa, and of the second oocytes into mature eggs and second polar cells, when it is reduced to one half the normal number. As spermatozoan and mature egg unite in fertilization, the original number of chromosomes is restored in the fertilized egg (zygote).

7. Fertilization

The stages concerned in a typical case of fertilization, according to Boveri, are illustrated in Figures 59 to 67.

In Figure 59 the "head" and the "middle piece" of the sperm-cell have penetrated into the egg cytoplasm, while in Figure 60 the tail of the sperm-cell has become lost and the middle piece, which furnished the centrosome, has rotated 180° so that it lies between the nucleus, or head, of the sperm-cell and that of the egg-cell. Figure 61 shows an increase in the size of the sperm nucleus and a division of the centrosome into two parts which begin to migrate towards the poles. This process of polar migration of the centrosomes is carried further in Figure 62 as well as the increase in the size of the sperm nucleus, until in Figure 63 the process is complete so that the centrosomes have assumed a polar position and the sperm nucleus is equal in size to the egg nucleus and lies in contact with it. In Figure 64 the chromatin network of the two nuclei has formed into an equal number of chromosomes which

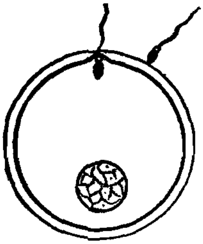

Fig. 59. *Entry of Sperm*

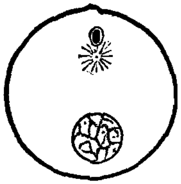

Fig. 60. *Loss of Sperm Tail*

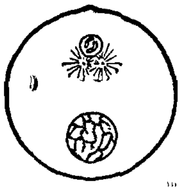

Fig. 61. *Division of Centrosome*

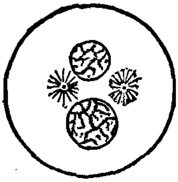

Fig. 62. *Approach of Sperm Nucleus*

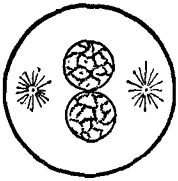

Fig. 63. *Increase of Sperm Nucleus*

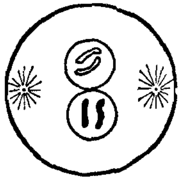

Fig. 64. *Formation of Chromosomes*

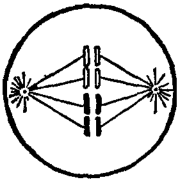

Fig. 65. *Splitting of Chromosomes*

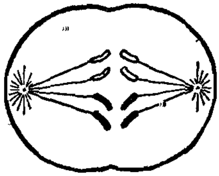

Fig. 66. *Anaphase*

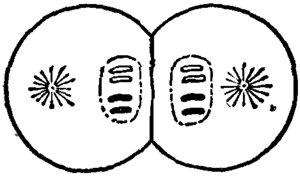

Fig. 67. *Two-celled Stage*

Figs. 59–67.—Diagrams illustrating fertilization. After **Boveri.**

in each case is half the number characteristic for the species. Figure 65 shows the complete disappearance of the nuclear membrane, a process that had already begun in the preceding figure, and also the arrangement of the chromosomes, connected with mantle fibers, in the equatorial plane where the former split longitudinally. In Figure 66, when the half chromosomes thus formed pull apart and migrate toward the poles, the segmentation of the fertilized egg has begun, and there finally occurs, as shown in Figure 67, the two-celled stage following fertilization in which each cell contains the normal number of chromosomes, half of which came from the egg and half from the sperm.

8. Parthenogenesis

Fertilization is by no means an essential process in the formation of a new individual, even in those animals which produce both eggs and sperm. Many animals and plants reproduce parthenogenetically, that is, the egg-cell may develop without first uniting with a sperm-cell. In these instances the chromosomes of the egg are not halved during maturation, and the offspring, therefore, have the same number of chromosomes as the parent, since they are simply fragments of the parent.

Professor Loeb, by the use of certain chemicals, has succeeded in doing artificially what apparently is not ordinarily accomplished in nature, namely, making an egg that normally requires fertilization develop parthenogenetically.

and, furthermore, when one passes in rapid review the marvelous array of characteristics which make up the sum total of what is obviously inherited in man, the wonder grows that so small a bridge can stand such an enormous traffic. A sharp-eyed patrol of this bridge as the strategic focus of heredity is proving to be one of the most effective points of attack in the entire campaign of genetics.

10. The Chromosome Theory

Certain investigators, who seek a morphological basis for heredity, regard the chromosomes as the carriers of the heritage; in other words, as the source of the determiners of ontogeny or the effective factors in the process of differentiation.

A few of the grounds for this theory are briefly indicated below.

First:. In spite of the great relative difference in size between the egg-cell and the sperm-cell, in heredity the two are practically equivalent, as has been repeatedly shown by making reciprocal crosses between the two sexes. The only features that are apparently alike in both the germ-cells are the chromosomes. The inference is, therefore, that they contain the determiners which are the causal factors for the equivalence of adult characters in heredity. The existence of an extra chromosome in probable connection with the matter of sex is, as will be pointed out later, an exception to the exact chromosome equivalence of the two sexes, which only goes to strengthen the supposition that the

chromosomes are the carriers of hereditary qualities since extra chromosomes are always associated with the character of sex.

Second: The process of maturation, which always results in halving the chromosome material of the germ-cells as a preliminary step to fertilization, is a series of complicated manœuvers not practised by other cells. During this process no other part of the cells appears to play so consistent and important a rôle as the chromosomes. Provided they act as hereditary carriers, their peculiar behavior during maturation is just what is needed to bring together an entire complement of hereditary determiners out of partial contributions from two parental sources.

Third: Sometimes abnormal fertilization occurs, as in the case when two or more sperm-cells, instead of one, enter the egg cytoplasm and unite with the egg nucleus. This unusual performance has been artificially induced by chemical means in the case of sea-urchins' eggs. The fertilized egg, or zygote, thus formed with an excess of male chromosomes, results in the development of abnormal larvæ. It is thought that a causal connection may exist, therefore, between the additional male chromosomes in the fertilized ovum and the abnormalities of the progeny.

Fourth: The fact that chromosomes may retain their individuality throughout the complicated phases of mitosis, as has been proven in some instances, agrees with the corresponding fact that certain characteristics of the somatoplasm maintain their individuality from generation to generation.

Moreover, certain chromosomes in the fertilized egg

have been identified with particular features in the adult developing from that egg. Tennent summarizes his work on Echinoderms (1912) by the statement that from a knowledge of the chromosomes in the parental germ-cells, particular characters in the adult hybrids may be predicted, and, conversely, that from the appearance of sexually mature hybrids the character of certain chromosomes in their germ-cells may be predicted.

Again, the correlation of a particular chromosome in the germ-cells with a definite adult character, namely sex, has been repeatedly demonstrated in connection with the so-called "extra chromosome" to which reference has already been made.

Fifth: Finally, excellent evidence of a definite causal connection between certain chromosomes of the germ-cells and particular somatic characters has been furnished by certain critical experiments upon the eggs of sea-urchins. Boveri found that he was able in some instances to shake out the nuclei bodily, chromosomes and all, from the mature eggs of the sea-urchin, *Sphærechinus*, and when there was added in sea water to such enucleated eggs the sperm-cells of an entirely different genus of sea-urchin, namely, *Echinus*, the Echinus sperm-cells entered the *Sphærechinus* eggs, which had been robbed of their nuclei, and from this peculiar combination larvæ developed which exhibited *only Echinus characters!*

Such cumulative circumstantial evidence as the foregoing has convinced many that in the chromosomes we have visibly before us the carriers of heredity.

In any event the supposition that the chromosomes,

with certain chemical reservations, are the morphological carriers of the heritage, forms an excellent working hypothesis, and this chapter may suitably be closed with a quotation from Professor Wilson, whose brilliant work in the entire field of cytology makes it possible for him to speak with authority. "In my view studies in this field are at the present time most likely to be advanced by adopting the comparatively simple hypothesis that the nuclear substances are actual factors of reaction by virtue of their specific chemical properties; and I think that it has already helped us to gain a clearer view of some of the most puzzling problems of genetics."

CHAPTER XI

THE ARCHITECTURE OF THE GER

1. Drosophila, the Biological Cinderella

Just as the bacteriologist firmly believes that guinea-pigs were specially created for serological experimentation, so the geneticist has come to realize that the banana-fly, *Drosophila melanogaster*, to which repeated reference has already been made, was designed for disclosing the secrets of the "architecture of the germ-plasm" (Weismann).

This tiny ubiquitous fly (Fig. 32), which hovers around bruised fruit without regard to place, is so small and harmless that it does not even qualify as a pest. It has proved, nevertheless, to be a veritable bonanza to the geneticist. It has many well-defined characters that can be observed under the microscope and it lives successfully upon a bit of banana in a milk bottle plugged with cotton. Every ten or eleven days a pair produces two to three hundred descendants that in turn are ready to produce similar families of their own so that the investigator who begins with them needs to be an expert bookkeeper in order to be able to record his results. Although, like Cinderella, *Drosophila* comes from the humble environment of the garbage can, yet this fly has easily outstripped all its sister competi-

tors for genetical honors, until to-day it stands probably as the most famous experimental organism in the whole world.

Prof. T. H. Morgan of Columbia University is the most conspicuous leader in the investigation of *Drosophila.* In his laboratory over ten millions of these animals, which literally "breed like flies," have passed in review under the microscope while pedigrees of over three hundred generations have been obtained and recorded. In no other plant or animal has the remarkable parallelism between the segregation of Mendelian characters in experimental breeding and the behavior of the chromosomes been so completely demonstrated.

2. Linkage

Drosophila has only four pairs of chromosomes although more than three hundred different characters have been found in the flies themselves, a fact which makes it at once evident that many genes, or character-determiners, must be located together in each chromosome.

Experimental breeding of *Drosophila* shows that there is not always complete independent assortment of the different characters that enter into a cross, as Mendel found to be true for the different characters of peas with which he experimented.

Genes located together in any one chromosome are likely to stay together during the conjugation of the chromosomes and the subsequent separation of the members of homologous pairs in the process of matura-

tion. This hanging together of neighboring genes of the same chromosome throughout the complicated process of meiosis is termed *linkage.*

It is extremely fortunate for the evolution of our knowledge of the mechanism of heredity that Mendel happened to work upon characters located in separate chromosomes and so was able to establish the law of the independent segregation of unit characters before the apparent contradiction, that is, linkage, became known. If he had come upon the confusing phenomenon of linkage first, the discovery of the laws of Mendelism, in all probability, would have been long delayed.

Bateson and Punnett called attention to linkage as early as 1906 under the name of "coupling" in the case of certain characters of sweet peas. A vague general knowledge of many groups of correlations, such as deafness and defective teeth going along with blue eyes and albinism in cats, had for a long time existed.

In *Drosophila,* the brilliant and extensive investigations of Morgan and his co-workers have resulted in definitely placing something like two hundred characters in four linkage groups corresponding to four pairs of chromosomes. The limitation of linkage groups to the number of chromosome pairs found in the organism is proving to be one of the fundamental principles of heredity.

Moreover, it has been shown by reciprocal crosses that linkage when it occurs is not due to some relation *per se* between the genes but simply to the fact that the linked genes chance to lie together in the same chromosome. In other words, if two characters enter a

cross together from one parent they will stay together in the offspring, and if they enter from separate parents, they remain separate in the offspring.

Male gametes / Female gametes	*GL*	*Gv*	*bL*	*bv*
bv	*GL* *bv*	*Gv* *bv*	*bL* *bv*	*bv* *bv*
bv	*GL* *bv*	*Gv* *bv*	*bL* *bv*	*bv* *bv*
bv	*GL* *bv*	*Gv* *bv*	*bL* *bv*	*bv* *bv*
bv	*GL* *bv*	*Gv* *bv*	*bL* *bv*	*bv* *bv*

FIG. 68.—Checkerboard to show the result of crossing a gray-long, black-vestigial hybrid fly back to a black-vestigial recessive. G = gray-body; L = long-wings; b = black-body; v = vestigial wings.

3. THE MODUS OPERANDI OF LINKAGE

The way linkage works out may best be made clear by illustrations from Morgan. When an ordinary wild-type fly with *gray body* and *long wings* is crossed with a fly showing the two mutations of *black body* and

vestigial wings, the hybrids of the first generation are all like the wild-type parent because gray body and long wings are dominant over black body and vestigial wings.

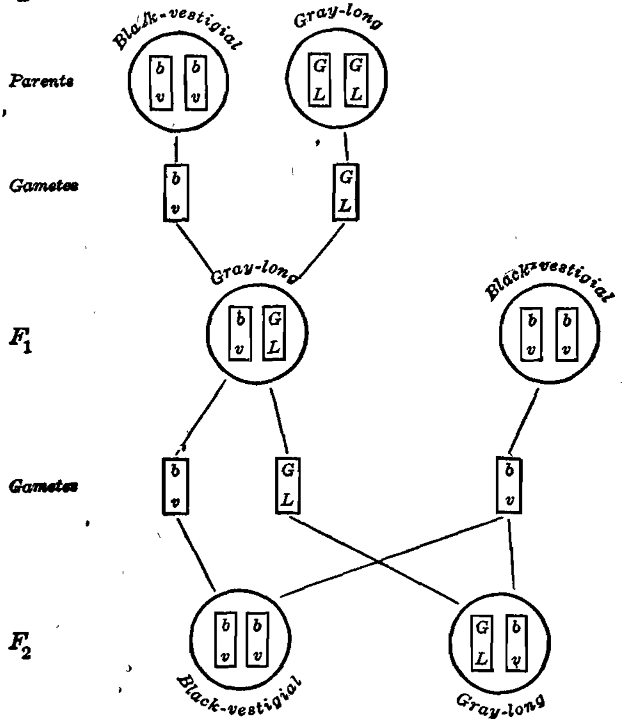

FIG. 69.—Typical linkage in *Drosophila*. Symbols as in Fig. 68. Data from Morgan.

When a male of one of these hybrid flies is crossed back with a recessive black-vestigial female, if Mendelian segregation took place there would be four possible kinds of offspring, as shown in Figure 68, viz., gray-

long; gray-vestigial; black-long and black-vestigial. The actual experiment, however, shows but two classes of offspring, viz., gray-long and black-vestigial, like the two grandparents (Fig. 69). In other words, gray-body and long-wings entering the cross from one parent stay linked together as do also black-body and vestigial wings. The method of crossing the hybrid back to the recessive is the common procedure in order to bring out what is latent in the hybrid, for the recessive, since it does not dominate or conceal anything, allows whatever is present in the hybrid being tested to appear. The Mendelian practice of crossing the F_1 hybrids together tends to conceal linkage and perhaps has prevented its earlier recognition.

The reciprocal cross is shown in Figure 70. In this case likewise, whatever goes in together comes out together and no new combinations appear.

4. Cross-over

When a gray-bodied long-winged *female* hybrid, such as is produced by crossing gray-long and black-vestigial together in the preceding experiment, is crossed back to a recessive black-vestigial *male*, there are produced four kinds of offspring, gray-long and black-vestigial like the grandparents and two new combinations, gray-vestigial and black-long. These four types of F_2 are what would be expected upon free assortment of all the gametes and they should all occur in equal numbers or in the proportion of 1 : 1 : 1 : 1. See Figure 68. Instead, as an actual result of extensive

crosses of this kind, Morgan obtained 41.5% each of gray-long and black-vestigial and 8.5% each of

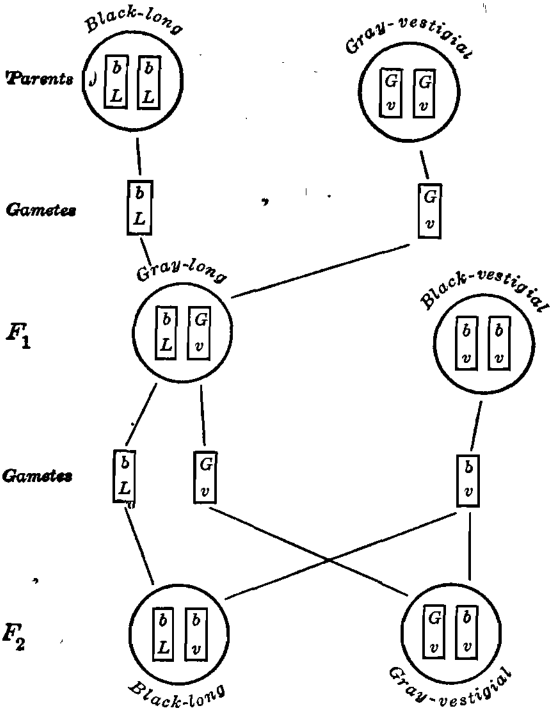

FIG. 70.—Typical linkage in *Drosophila*. Reciprocal to the case shown in Fig. 69. Data from Morgan.

the new combinations of black-long and gray-vestigial. (See Figure 71.) The new combinations represent *cross-overs* or breaks in the linkage of the genes within the chromosomes.

Although this superficially resembles the free assortment or segregation of typical Mendelian crosses, it

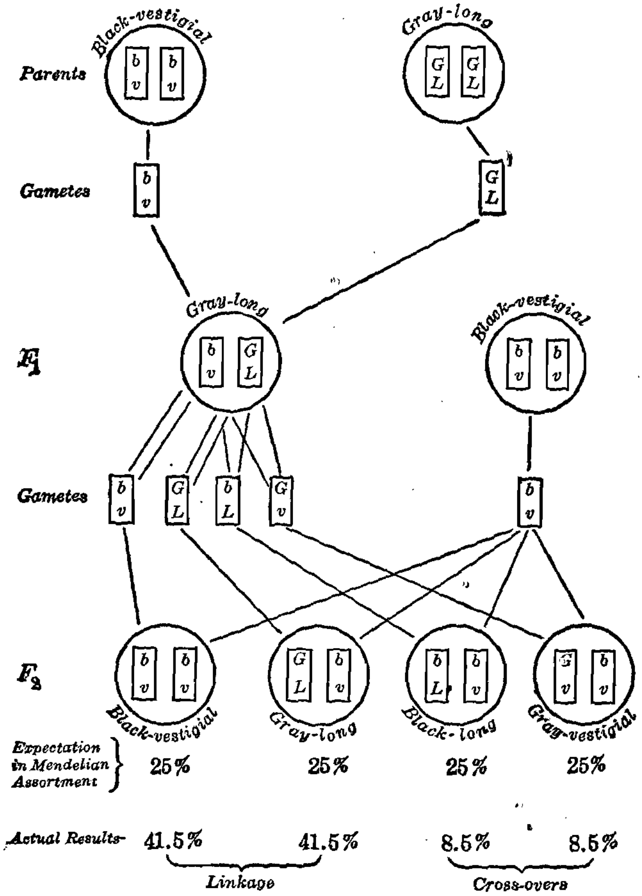

FIG. 71.—Typical cross-over in *Drosophila*. Symbols as in Fig. 68. Data from Morgan.

is quite a different thing since Mendelian segregation involves whole chromosomes while cross-overs involve only parts of chromosomes. The percentage too of the

different classes resulting in the F_2 generation from hybrids is different in typical Mendelian segregation and in cross-overs.

Furthermore, the percentage of cross-overs varies in different crosses. For example, when white-eyed yellow-bodied flies are crossed with normal wild-type red-eyed gray-bodied individuals, the resulting hybrids resemble wild red-eyed, gray-bodied flies. When such a female hybrid is crossed back to a recessive white-eyed yellow-bodied male, the offspring show only one per-cent of cross-overs, that is, white-eyed, gray-bodied and red-eyed, yellow-bodied individuals, and 99% of linkage, that is, white-eyed, yellow-bodied and red-eyed, gray-bodied (Fig. 72).

Another percentage of cross-over, that between *white-eye and miniature-wing was found to be 33. It is* obvious that in any case the cross-over will never exceed 50%.

Jennings has said: "The studies of 'crossing-over' promise to bring us into closer touch with the actual details of the hereditary mechanism than any other phenomena now under examination."

5. How do Cross-overs Occur?

In germ-cells before maturation, homologous maternal and paternal chromosomes pair off and usually come to lie side by side. This is the phenomenon of *syndesis* or conjugation. During this temporary contact there seems to be an opportunity for such an exchange of parts as cross-over breeding demonstrates does actually

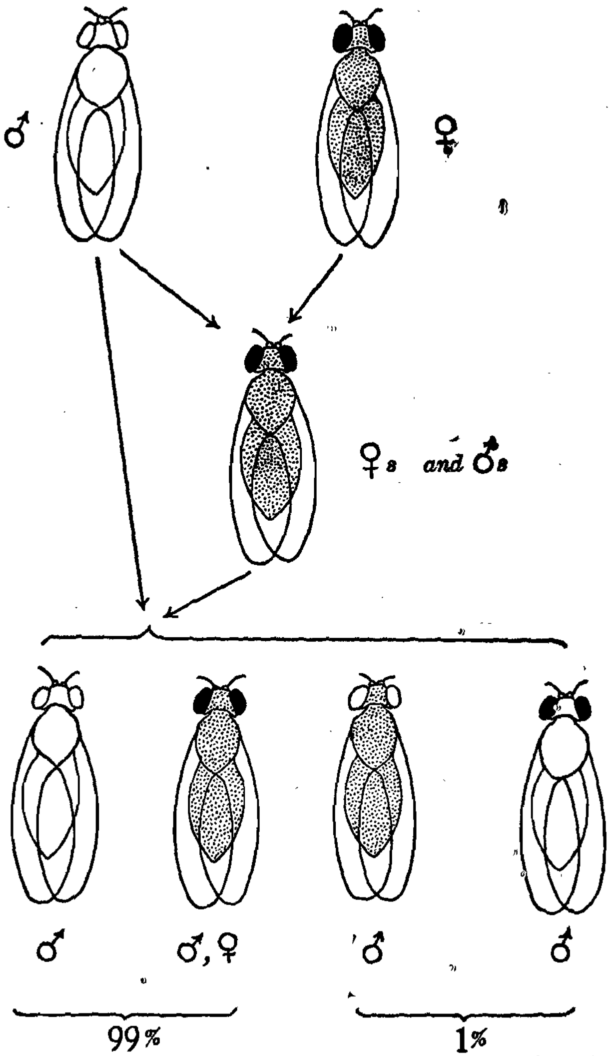

FIG. 72.—A case of one percent cross-over in *Drosophila*. Gray-body and red-eyes are represented by stippling and solid black respectively. Yellow-body and white-eyes are unshaded. After Sharp, from Morgan's data.

occur. Syndesis has been repeatedly observed and sometimes two chromosomes are seen even to twist about each other. When separation comes after this embrace the two original chromosomes may simply unwind and to regain their former condition unchanged, or they may break and fuse in such a way that one (A) has a part of the other (B), and the remaining parts show a corresponding fusion, as indicated in Figure 73.

This is the chromosomal explanation (*Chiasmatype*

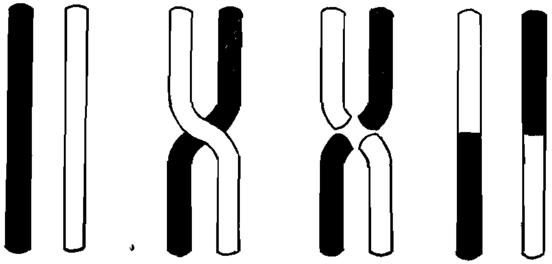

FIG. 73.—Diagram to show cross-over between two homologous chromosomes. After Muller.

theory of Janssens) of the cross-over phenomena known to the experimental breeder.

6. INTERFERENCE

The varying percentages of cross-overs between different pairs of genes led Morgan and his associates to attempt the localization of genes within the chromosomes. The idea, as suggested by Bridges in 1914, is simply this, that the farther apart two genes are in the chromosome the more likely they are to cross over and to "exchange" places with their homologous genes during syndesis.

Of course if they lie very close together in the chromosome they are apt to be found finally on the same side regardless of the twisting of the paternal and maternal chromosomes about each other. This is evident in Figure 74 where the invisible genes are represented hypothetically by letters placed within the chromosomes. Cross-over is more likely to occur between A and E which lie at the extremes of chromosome I than between A and B which are closer together.

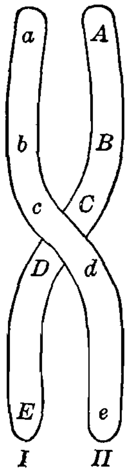

Fig. 74.—Interference. Two homologous chromosomes during syndesis. When there is a cross-over between Cc and Dd, it *interferes* with another cross-over near by between Cc and Bb.

Again, when genes lie close together they theoretically interfere with the crossing over of neighboring genes as pointed out by Muller and confirmed by subsequent breeding experiments. In Figure 74, for example, if crossing-over took place between the pairs Cc and Dd, breaking the linkage between C and D and between c and d, it would prevent another break of linkage between BC and bc. This is the phenomenon of *interference.* It follows that the nearer together two pairs of genes involved in cross-over are located, the greater will be the interference.

7. The Arrangement of the Genes

Morgan assumes that if one per cent of cross-overs occurs this may be made to represent one arbitrary unit of distance between the two genes in question. Haldane proposes to call this unit of cross-over a *morgan*. In the illustration of black-body and vestigial-wing where there was 17% of cross-over it is assumed that the genes for these two characters are 17 units, or morgans, apart in the chromosome.

Following up this fertile idea it becomes possible even to map the location of the genes in the chromosomes. Sturtevant was the first to make such a map for the genes in the "sex chromosome" of *Drosophila.*

This has been followed by maps of the other chromosomes, after breeding a total of several million flies and analyzing the data which include altogether the behavior of over a hundred different genes.

The *relative location* of the genes has been determined by the following method. If for example two genes, A and B, upon breeding back to the recessive show 5% of cross-overs with a and b, while B and C show 20% with their allelomorphs, b and c, then when A and C are bred together with a and c, they should give either the sum $(5 + 20 = 25\%)$ or the difference $(20 - 5 = 15\%)$ of cross-overs.

For example, in an actual experiment, yellow-body and white-eye gave 1.2% cross-overs while white-eye and bifid-wing gave 3.5% cross-overs. When yellow-body and bifid-wing were tested they met the expecta-

tion and gave 4.7%, or the sum of the other two pei centages, as shown in Figure 75.

If upon breeding yellow and bifid a percentage o 2.3% had been obtained instead of 4.7% as was ac tually found, then the order of the genes would hav been yellow-bifid-white instead of yellow-white-bifid

In the eloquent frontispiece of *The Mechanism o Mendelian Heredity*, by Morgan, Sturtevant, Bridge and Muller, there are drawn four straight parallel line representing the "chromosome maps" of *Drosophil*

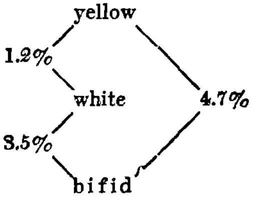

FIG. 75.—An illustration of the proof of gene-localization from cross-over percentages obtained by breeding.

as known in 1915. It is doubtful if in any book there may be found four straight lines that mean so much. The work of gene-localization is quite comparable to that done by mathematicians and astronomers in determining the distances that separate the stars in the heavens from each other and is perhaps equally incomprehensible to the layman. In gene-localization it is the infinitely small instead of the infinitely great that one must observe. When it is remembered that *Drosophila* is a very tiny fly; that occupying only a small part within its abdomen are paired reproductive organs; that each of these reproductive organs in the

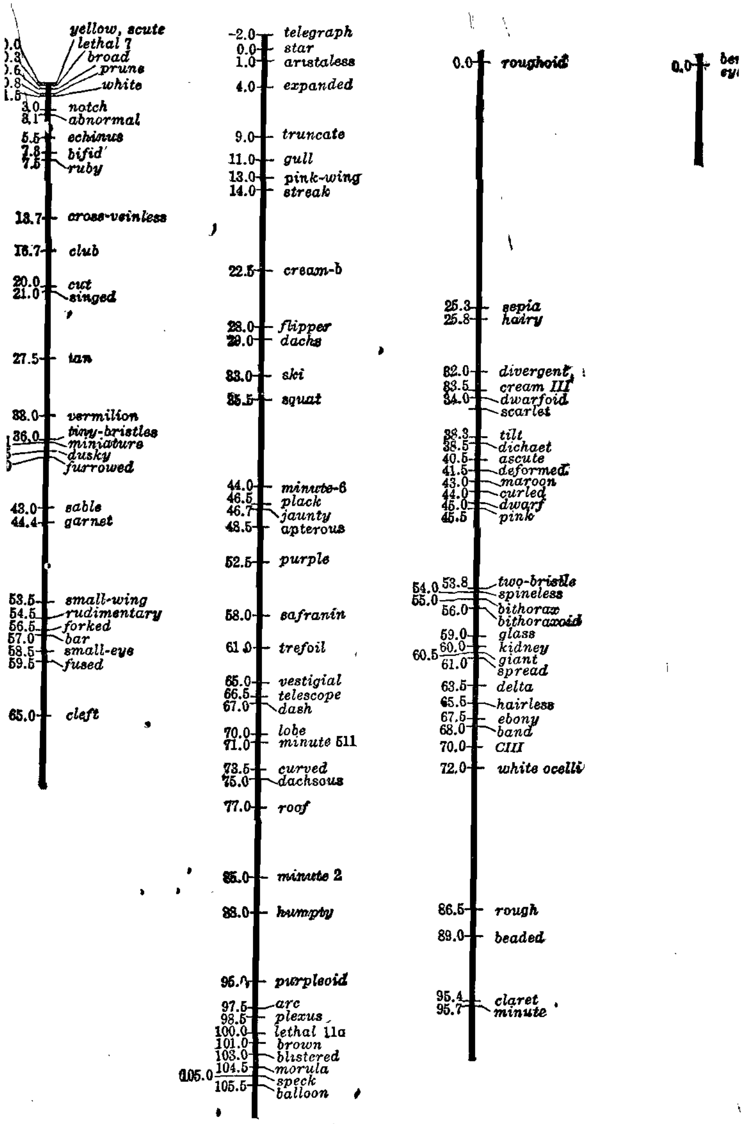

FIG. 76.—Chromosome maps of *Drosophila.* **After Sharp.**

male is made up of several tubules; that within these tubules may eventually be found the sperm cells with plenty of room to move about; that within a single sperm cell is the nucleus; that after half of the contents of the nucleus has been disposed of there remain four chromosomes; that within each chromosome beyond the range of vision there are hundreds of genes and that it has been possible in a single chromosome to determine not only the relative arrangement of over thirty genes but also to find out the relative distance between these genes, it will be realized that the analysis of the germplasm has gone a long way.

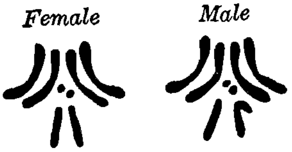

FIG. 77.—The chromosomes of *Drosophila melanogaster*. After Bridges.

In Figure 76, taken from Sharp's "Introduction to Cytology," are represented the four chromosome maps of *Drosophila* corrected to November, 1920.

The four visible chromosomes of *Drosophila* correspond to the four linkage groups of characters obtained by experimental breeding and it is a striking fact that no character has yet appeared that cannot be assigned to one of these four linkage groups. The relative length of the four "maps," which has been determined from the carefully worked-over data acquired by years of riotous breeding for cross-overs, agrees remarkably with the relative differences in the actual size of the chromosomes as measured under the microscope. The four pairs of chromosomes in a male *Drosophila melanogaster* are represented in Figure 77.

8. Linkage in Other Organisms

The phenomenon of linkage has already been observed in various other organisms besides *Drosophila.* Even in Mendel's classic peas White demonstrated four linkage groups of characters and seven pairs of chromosomes. It is doubtful if Mendel himself ever heard of chromosomes for he died in 1886 and Boveri's pioneer work on chromosomes had only then recently appeared. A list of a few of the organisms in which linkage has been reported is given below.

Organisms that show linkage	*Author*
Sweet pea	Bateson and Punnett
Snapdragon, Wheat	Baur
Primula	Altenberg. Gregory
Maize	Emerson. Breggar. Lindstrom. Jones
Tomato	Jones
Beans. Oats	Surface
Evening primrose	Shull
Drosophila virilis " buscki " repleta	Metz
Silkworms	Tanaka
Grouse locust	Nabours
Pigeon	Cole and Kelly
Rat. Mouse	Castle and Dunn
Rat	Ibsen
Rabbit	Castle

CHAPTER XII

SOMATOGENESIS

1. The Hereditary Tunnel

The earlier studies in heredity were concerned with the comparison of successive individuals, or somatoplasms. This phenotypic method has attained a considerable degree of success through the analysis afforded by Mendelism.

A different and still more recent method of attack upon the problem of heredity deals not with individuals but with chromosomes which are generally acknowledged to be the living springs from which flow the streams of inheritance. Such an intensive cytological study of the germplasm has revealed a mechanism that explains to a marvelous extent the results of the experimental breeder.

The demonstration of the parallel between the behavior of the germplasm as seen in the chromosomes and the performance of the somatoplasm as exhibited in the end results of experimental breeding, is one of the most impressive scientific achievements of our times.

There is an undoubted causal connection between the genotype and the phenotype at the extremes of the hereditary pageant but between these extremes, that is, between the fertilized egg and the adult, investigators are as yet by no means as confident or well-informed.

It is as if heredity was represented by a long underground tunnel. We are in the light at either end and have made out to a considerable degree the details at the entrance and exit, but we are still largely in darkness throughout the passage-way itself.

The science of embryology has given us a series of flash-light pictures of what goes on in the tunnel of development but of necessity its contribution has been largely morphological. Consequently the geneticist still awaits some torch-bearer who will reveal how an invisible gene within a chromosome can give form and substance to a definite visible unit character in an organism. Probably genetics has contributed more to embryology than embryology to genetics in the past but it is quite likely that the account will be more than balanced in the future.

The way in which germ-cells come by their potent hereditary components, rather than how they make use of them, has been the first and most natural problem to engage the attention. The solution which satisfies most biologists, who have considered the evidence, has been found in the idea of the *continuity of the germ-plasm*, that is, that hereditary genes are not the product and result of the body carrying them but are lineal descendants of ancestral genes which have been housed temporarily in other bodily domiciles in the past.

The familiar miracle of how hereditary genes work together to produce a new plant or animal is farther from a satisfactory solution, yet there is no doubt that some of the impending great discoveries in genetics are sure to be exactly in this field.

2. Preformation and Epigenesis

How does germplasm transmute into somatoplasm? Historically there have been two conspicuous attempts to solve the riddle of differentiation, neither of which gives intellectual satisfaction any longer in the light of what is known to-day.

The first held sway in the 17th and 18th centuries under the guise of the *preformation theory* which assumes that development is simply the unfolding and enlarging of what was already present in the germ in miniature. This has been called the theory of "emboitement" or "infinite encasement," because, not only is the miniature plant or animal supposed to be packed within the germ-cell like the embryo plant between the cotyledons of the bean seed, but within each miniature also it is supposed that the next generation is encased, and the next, *ad infinitum*. Aided by a poor microscope and a good imagination the theory of preformation was carried to such an extreme that a mannikin or "homunculus" was actually figured by Hartsoeker seated within the head of a human spermatozoan!

The second attempt to solve the riddle of development resulted in the theory of *epigenesis* which goes to the other extreme, maintaining that organization gradually appears out of an absolutely simple undifferentiated germ. This theory had its most influential exposition in "Theoria Generationis" by C. F. Wolff in 1759. "The mistake in the doctrine of preformation was in supposing that germinal parts were of the same kind as adult parts; the mistake of epigenesis was in maintaining a lack of specific parts in the germ."

(Conklin). Neither of these two conceptions is in accordance with the facts as known to-day.

3. What is Somatogenesis?

Development is not simply the unfolding or assortment of what is already present in the germ nor is it the miraculous writing of something new upon a clean slate. Rather it is the orderly initiation and sequence of new structures and functions conditioned by the interaction of the germinal elements present in the egg or ovule.

Thus *somatogenesis* is the study of the emergence of bodily structure out of hereditary sources. Like the evolution of species, which has so enthralled the minds of thinking men, somatogenesis in a parallel way is the evolution of the individual. No doubt each of these epic histories will eventually furnish the key and vocabulary to the other.

Both somatogenesis and gametogenesis, which concerns the origin of the germ-cells themselves, are cytological in their terminology, and are referable to the germplasm (see Figure 78), as contrasted with the Mendelian and biometric aspects of genetics which are not primarily cytological but are, on the contrary, statistical in method, dealing directly with somatoplasms.

4. The Factors in Somatogenesis

Somatogenesis deals with the interaction of at least two sets of factors, viz., (1) hereditary, and (2) environmental.

Hereditary factors have been described and have received the major share of attention in the preceding pages. Environmental factors may upon occasion,

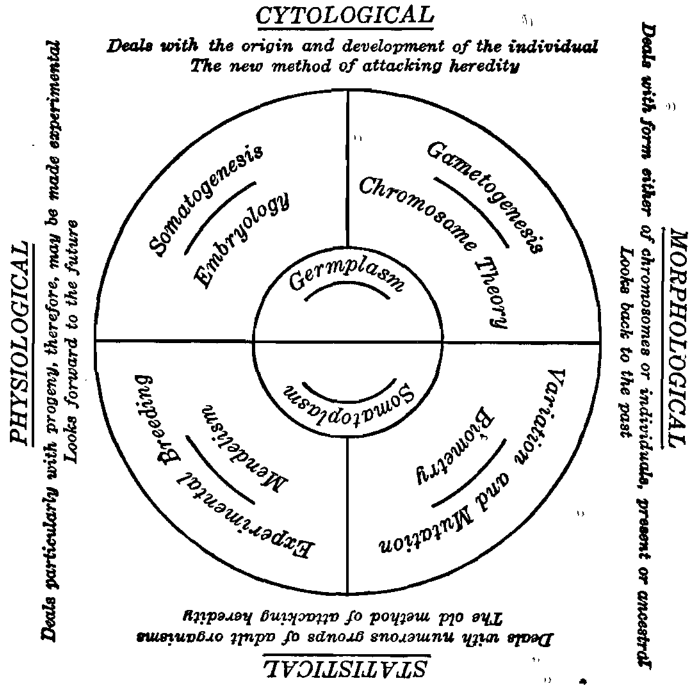

FIG. 78.—Any-side-up Diagram of Genetical Sciences.

however, cause enormous modifications in somatogenesis although the limits of variation are set by hereditary genes. For example, genes under any environmental circumstances whatsoever never allow an egg with the heritage of a worm to develop into a bird, nor do human

genes freighted with the handicap of idiocy ever produce an intellectual leader.

5. The Rôle of Genes in Somatic Differentiation

An essential feature of cellular differentiation is the unequal division of material, both quantitatively and qualitatively. When we trace the complicated adult organism backward step by step to the fertilized egg from which it started we see that its complexity has arisen largely through this process of unequal division.

Moreover, each stage in the "process of becoming" is conditioned upon what has already happened in preceding stages, since differentiation is a forward-moving sequence of events. Just as the roof of a house must follow and not precede the erection of walls which are placed on a foundation previously prepared, so the hereditary matter in the gene must pass through a long series of preliminary steps of differentiation before finally coming to manifest fruition in the soma.

Weismann, who by the process of logic rather than experimentally located the germinal substance in the nucleus of the germ-cell, assumed an elaborate theoretical system of "biophores," "ids," "idants," etc., whereby a differential distribution of the nuclear substance of the germ-cells to the various somatic cells is supposed to occur. This is diagrammatically shown in Figure 79.

Subsequent discovery and confirmation of the facts of mitosis, however, have shown that the germplasm does not influence the development in this way, for

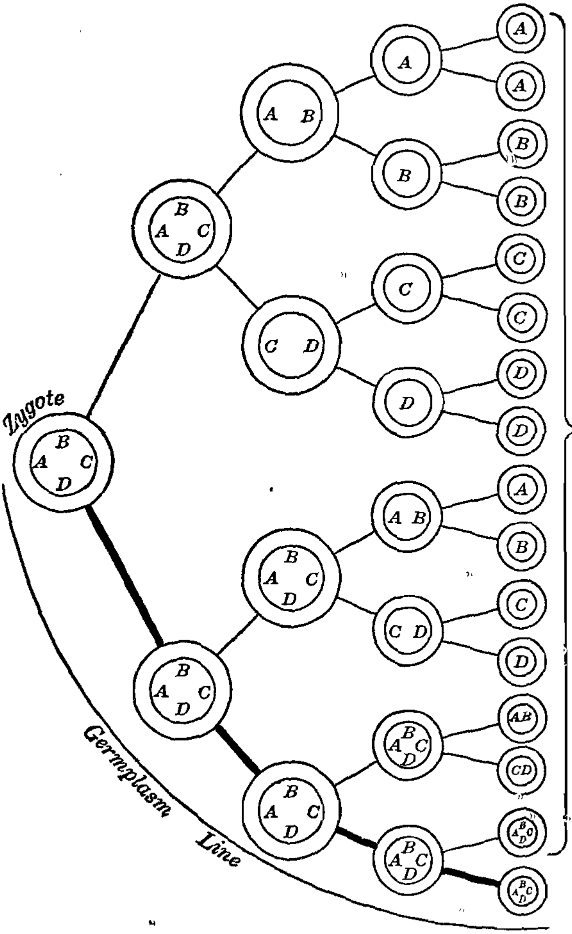

FIG. 79.—Differentiation in somatogenesis according to Weismann. Modified from Conklin. The large outside circles represent cytoplasm, the inside circles the nuclei. Differential distribution of nuclear substance.

everything indicates that the entire machinery of mitosis is directed toward securing an *equal division* of the heredity-determining chromatin to the two daughter-cells at each division. Ordinarily the entire

chromatic complex is handed down from cell-generation to cell-generation in the development of the soma regardless of the type of tissue to be formed. The question now logically follows:—How can identical germinal substance give rise to different products in different cells? How can a nerve cell, for example, so depart from its embryonic spherical form that its cytoplasm becomes drawn out into enormously attenuated neurones tingling with neuro-fibrils, while a cartilage cell, with the same outfit of germinal determiners in its nucleus, commits cytological suicide by the excessive secretion of its cell wall?

DeVries in his theory of "intra-cellular pangenesis" (1889) proposes, as a way out of this dilemma, *enzymatic "pangenes,"* of which each nucleus contains a complete set, that escape into the cytoplasm and so control its differentiation,—an explanation "which nearly meets the present requirements and fits present knowledge." *It is the cytoplasm and not the nucleus that differentiates,* although the directing stimulus for differentiation comes from the nucleus.

This conception is diagrammatically shown in Figure 80, which figure, furthermore, explains how the stamp of the germplasm upon the somatoplasm can influence not only immediate cell-division but all subsequent ontogenetic divisions until the adult structure results.

6. "Cytoplasmic Inheritance"

While the germinal determiners in the chromosomes are being apportioned to the daughter cells in mitosis with strict impartiality, the cytoplasm surrounding

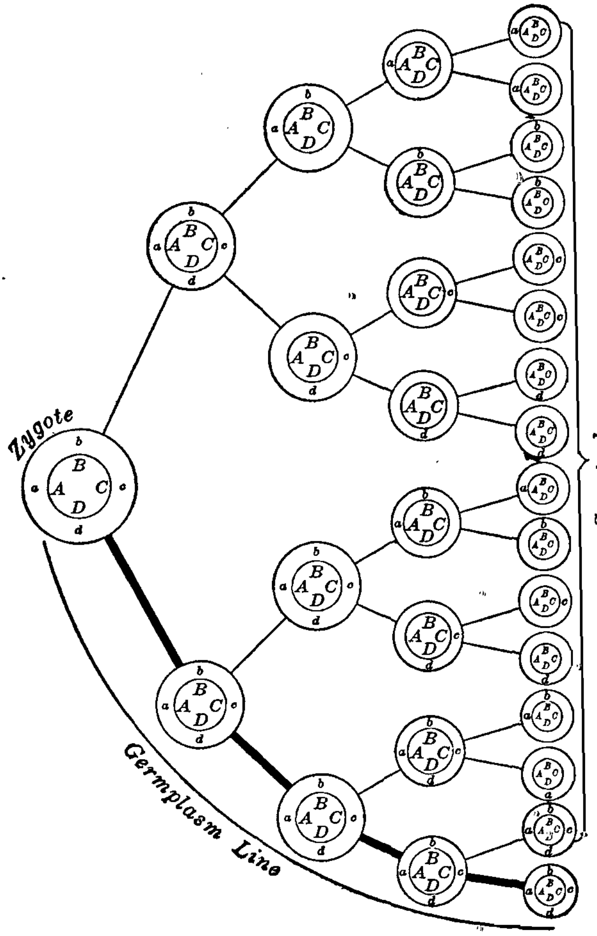

FIG. 80.—Differentiation in somatogenesis according to deVries. Modified from Conklin. The large outside circles represent cytoplasm, the inside circles the nuclei. The cytoplasm differentiates, not the nucleus.

the nucleus does not meet the same fate. The unequal distribution of the cytoplasm, even in the early cleavage stages of somatogenesis, is quite apparent. Moreover,

in the cytoplasm of the fertilized egg of many forms qualitative differences may already be detected that prophesy clearly the course which differentiation is to take. Conklin cites the illuminating case of the ascidian *Styela,* in whose egg the cytoplasm in different regions varies distinctively in color so that these parts may be unquestionably followed in subsequent cleavage and their fate definitely discovered.

For example, the peripheral area of the cytoplasm of this egg containing yellow coloring matter finds its way into the cleavage cells which become muscles and mesoderm; a gray area is differentially assorted into cells that become nervous system and notochord; a slate-blue part proves to be the source of epidermal cells and a region of colorless substance gives rise to ectoderm cells.

Most egg-cells are more reticent than *Styela* in revealing the part that their cytoplasm is to play in ontogenesis, but it has been possible in many instances to trace cell-lineage through the cleavage stages until the results of differentiation are unmistakable in the tissues.

The fact that so many eggs clearly show polarity and indicate the future symmetry of the organism before development has begun at all is further evidence of the important part that the cytoplasm plays in somatogenesis. For example, when the fertilized frog's egg divides for the first time into the two-cell stage these two cells are the ancestors of the right and left sides of the animal and the cleavage plane between them marks the future long axis of the body.

Thus while the chromosomes with their invisible genes are the ultimate determiners of heredity, the enveloping cytoplasm that surrounds the nucleus, particularly of the egg-cell, may be the immediate arbiter of the differentiation processes that characterize somatogenesis. "In short," as Conklin says, "the egg cytoplasm determines the early development and the sperm and egg nuclei control only the later differentiations. . . . The chromosomes are chiefly concerned in heredity, the cytoplasm in development."

There is nothing in what has been said of "cytoplasmic inheritance," however, to conflict with the generalization that the real determiners of heredity are germinal, for it is the genes in the nucleus of the parent germ-cell that gives the character to the egg of the daughter-cell, both to its nucleus and to its cytoplasm, although the latter in turn influences particularly the early stages of somatogenesis. In an excellent criticism of the rôle of nucleus and cytoplasm as vehicles of heredity, Dunn [1] concludes:—"For development, its mechanism is but grossly known, but we have learned enough of the determinative effect of the nucleus and of the possibilities of interaction between cytoplasm and nucleus to foster a suspicion that one day the governance of the chromosomes over development will be explained in physical terms."

7. The Physical Stage-setting

During development the organism is beset on all sides by various external physical factors, which are more

[1] *Amer. Nat.* vol. LI, 1917, p. 286.

or less necessary to its life, and the modification of these factors brings about a corresponding variation in the normal progress of somatogenesis.

These external factors, such as temperature, moisture, light, chemical solutions, pressure, etc., may accelerate, retard or even inhibit the normal course of events, but invariably such external environmental factors contribute largely to the end result of somatogenesis.

It is quite likely that many kinds of monsters and defective organisms are the result not of defective heredity but of alterations in the normal constellation of physical factors which constitute the environment of the developing organism.

8. The Internal Environment

Not only is somatogenesis hedged about by external modifying factors but there is also an internal environment that controls to a large degree the behavior of hereditary factors and determines how they shall come to expression in the somatoplasm.

The obvious way in which growth is dependent upon the intake and use of food, and the abnormal outcome following an unnatural chemical situation within the body, such as the presence of poisons, are illustrations of what is meant by internal environment. Perhaps the best illustration of this is furnished by the endocrine glands in mammals. Twenty years ago very little was known with certainty about the part that these ductless glands play in the organism, but they have become so

important in modern medical research that ***endocrinology*** is now recognized as a very lusty infant in the family of biological sciences.

The chief endocrine structures in man are the thyroids, parathyroids, the two functionally and anatomically distinct lobes of the pituitary gland, pineal gland, thymus, adrenal glands, portions of the pancreas and the various sex glands (testes, prostate, ovaries, etc.). These structures are *physiological regulators* and have to do with the growth and development not only of the body but also of the mind. Human instincts, emotions, mental and psychic states are stimulated, inhibited, altered and complicated by endocrine action. The endocrines, therefore, constitute a large part *of the machinery through which heredity must act* to bring about its results and consequently it is possible to control, to a considerable extent, the development and behavior of man through the internal secretions produced by these glands. "Some people are born with so stable an endocrine relation," says Bandler, "that nothing will alter the normal interaction of the endocrine glands; others inherit or acquire endocrines so unstable or deficient that nothing else can elevate them to the threshold of the normal."

9. The Rate of Development

No doubt one essential feature in the development of an organism is differentiation or the unequal assortment of material as already mentioned in a preceding paragraph, but another factor in somatogenesis is

surely the time element as it appears in the acceleration or retardation of the processes concerned. Not all tissues or organs develop at the same rate. Some outrun others necessarily in order to prepare the way for what follows. Under normal conditions in ontogenesis things swing into place in the nick of time to make the next step possible. When these rhythms are upset, just as when Field Marshal Grouchy at Waterloo failed to swing his troops into line at the critical moment, then there results a Waterloo in the organism. To any one who has followed in detail the intricate stages of ontogenesis in some organism, conditioned as it is by its indispensable and modifiable environmental complex, the wonder grows that the successes are so many and the disasters so few.

10. Conclusion

It is not enough for the geneticist to know the chromosomal machinery at the beginning of his story and the Mendelian moral at the end of it. Between these two fields of investigation lies the no-man's land of somatogenesis which forms an important part of the hereditary tale.

The processes of somatic differentiation are so amenable to experimental interference that no doubt future investigators will continue to be attracted to the cultivation of this promising field of genetics.

CHAPTER XIII

THE DETERMINATION OF SEX

1. Prevalent Ideas

The mechanism of sex determination has been a matter of speculation since time immemorial and many erroneous as well as impossible ideas remain even to-day in the mind of the layman. These speculations fall into three categories, according to whether the belief is held (1) that the sex of the offspring is predetermined in the egg; (2) that it is determined at the time of fertilization; or (3) that it is not determined until after the zygote has been formed.

All the older experiments on sex were based on the last of these suppositions. It was believed that by varying the nutrition of the developing embryo either sex, as desired, could be obtained. This belief was applied even to human beings. Experiments on tadpoles seemed to give definite positive results, but we now know that the death rate in these experiments was so large that the results may be more truly explained as due to differential mortality.

Others held that the age or vigor of the parent determines the sex, the older or more vigorous of the two parents tending to impress its sex upon the offspring.

Yet another belief, and one still held by many, re-

gards the freshness or staleness of the egg as the important factor in predetermining sex. According to this idea it is thought that an egg shortly after ovulation tends to produce a female, while one that remains some time in the oviduct tends to produce a male.

The idea that two distinct types of eggs are formed is not altogether new. Thus, entirely without biological foundation, the theory has been propounded that one ovary gives rise to male-producing eggs and the other forms female-producing eggs. Equally without foundation is the theory that in one testis male-determining spermatozoa are produced and in the other, female-determining spermatozoa.

Modern theories of sex determination hold to the first and second of the three possibilities mentioned above. If there are two kinds of eggs, male-producing and female-producing, then the sex of the individual is already fixed at the time of the extrusion of the first polar cell, before the sperm-nucleus has united with the egg-nucleus in fertilization. If there are two kinds of sperm, male-determining and female-determining, then sex depends upon the type of sperm uniting with the ovum, and it may, therefore, be said that sex is determined at the time of fertilization.

2. Sex Chromosomes

Our present day stand on sex determination is based entirely on direct observation, both cytological and experimental. In 1902, an unpaired chromosome was observed by McClung in the testes of certain Orthoptera.

This he called a sex-determiner. The association of this chromatic body with sex determination proved to be a discovery of primary importance. In fact it opened a new era in cytology and heralded the beginning of a large number of experiments and much profitable discussion dealing with the mechanism of sex determination.

In many groups of animals there is an unpaired chromosome in the male, called the *x*-chromosome, which may be seen in the somatic cells, in the spermatogonia and in the spermatocytes (Fig. 81). In the female cells, both somatic and germinal, the *x*-chromosome is paired. During the process of spermatogenesis the *autosomes*, that is, the remaining chromosomes which have nothing to do with the determination of sex pair to form *tetrads*, in the first spermatocyte division, but are later reduced to *dyads*, in the second spermatocyte division, when the *x*-chromosome passes undivided to one of the second series of spermatocytes (Fig. 81). The other spermatocyte of the second division accordingly receives no part of the sex-determining material. During the division into spermatids the former second spermatocyte, now freighted with the *x*-chromosome, gives rise to *x*-bearing cells which form the female-determining sperm, while the other second spermatocyte, which did not receive an *x*-chromosome, gives rise to two male-determining spermatozoa.

Hence, any zygote receiving two sets of autosomes and two *x*-chromosomes becomes a female, while a zygote receiving two sets of autosomes and only one

x-chromosome becomes a male. Since both types of sperm are ordinarily formed in equal numbers, the

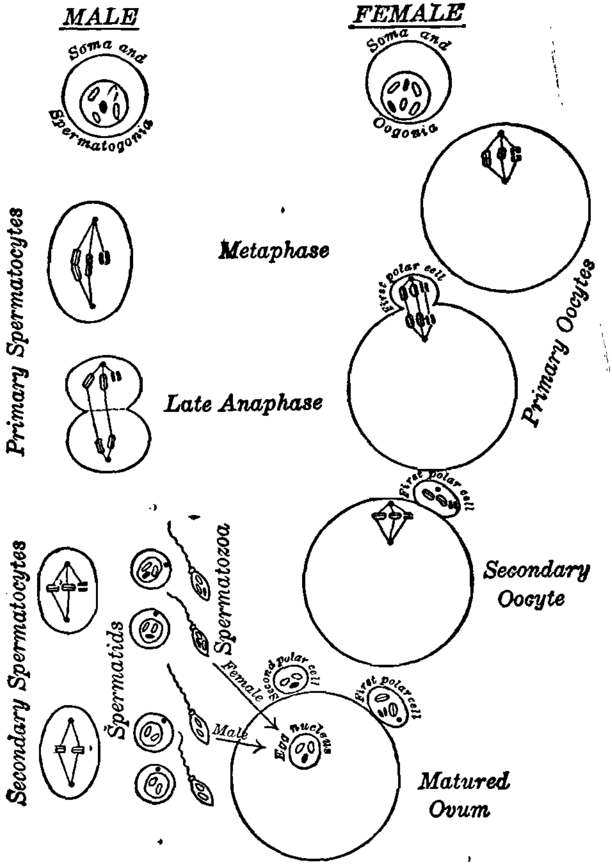

Fig. 81.—Sex determination in the case of heterogametic **males.**

chances that a male- or a female-determining sperm will reach the egg in the process of fertilization, are

equal and the resulting zygotes, therefore, are approximately 50 per cent male and 50 per cent female (Fig. 82).

A. THE Y-CHROMOSOME

The foregoing is the simplest case of sex-determination known and, while this is the fundamental type, still there are many variations of the mechanism. For example, the x-chromosome may have a "y" partner in the male cells, in which case, if n = the haploid, or

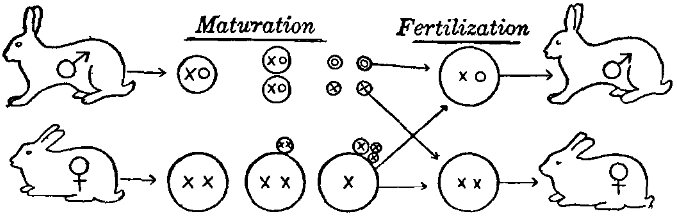

FIG. 82.—Diagram to show how numerical eqaality of the sexes results when one parent is homozygous (the female in this instance) and the other is heterozygous for the sex character.

halved, set of autosomes in a given animal, then the following formula holds true:—

$$2n + xy = \text{male and } 2n + xx = \text{female.}$$

In the spermatogonia of animals maturating in this manner, half the spermatids receive an x-chromosome and half a y-chromosome, the latter being the male-determining spermatozoa.

In certain other cases the x-chromosome may be represented by several discrete, *i.e.*, separate, components, and it may or may not have a y-chromosome

associated with it in the male cells. Thus, in *Gelastocoris*, a hemipteron, the male is represented by the formula $2n + 4x + y$ and the female by $2n + 8x$. Here "n" equals fifteen, so that the male diploid number of chromosomes is thirty-five and the female, thirty-eight.

Until recently the y-chromosome has not been known to carry specific genes for bodily characters. Indeed, this chromosome has been generally regarded as merely a degenerate x-chromosome that has lost its sex genes and most of its other genes as well. That it is essential to the typical development of those species where it is normally present has been proven in the non-disjunction experiments of Bridges. A male *Drosophila* without the y-chromosome, for instance, is sterile.

In many forms it is not unlikely that there is no sex-determining mechanism visible even with the aid of the best microscopes, but, nevertheless, it is probable that x- and y-chromosomes exist, and that the y-chromosomes are practically equal to the x-chromosomes in size, differing from them merely in the absence of specific genes.

B. SEX GENES

In the female, except in those cases where difference in chromosomal size is present, the x-chromosomes cannot always be distinguished from ordinary autosomes and it is furthermore known from breeding experiments that they bear many genes for characters having nothing to do with sex.

That there are specific genes in the y-chromosome which, working in conjunction with autosomal genes are capable of producing males, females or intermediates, in cases where the normal relationship is upset, has been indicated very clearly, especially by Bridges in recent experiments on *Drosophila.*

Sex, in other words, is now put upon a basis of specific genes. We are, therefore, entirely rid of the older ideas that the x-chromosome is composed of a different kind of chromatin from that found in the autosomes and that the sex of the zygote depends upon the *amount* of x-chromatin it receives.

C. HETEROGAMETIC FEMALES

The reverse of the foregoing mechanism, in which two kinds of sex-determining sperm are present, is found in the *Lepidoptera* and birds. In these groups the presence of $2n + xx$ constitutes a male and $2n + x$, a female. The formulæ in these cases are usually written $2n + zz$ and $2n + z$, in order to distinguish them from those of heterogametic males.

The cytological proof for the z-chromosomes is not as strong as for the x-chromosomes, since both avian and lepidopteran chromosomes are peculiarly difficult to study. Nevertheless, the facts are well borne out by breeding experiments in both groups.

Definite results have been reached by Seiler and also by Doncaster in experiments with moths, showing that two types of ova are produced, namely, one which, after extruding the z-chromosome into the polar cell

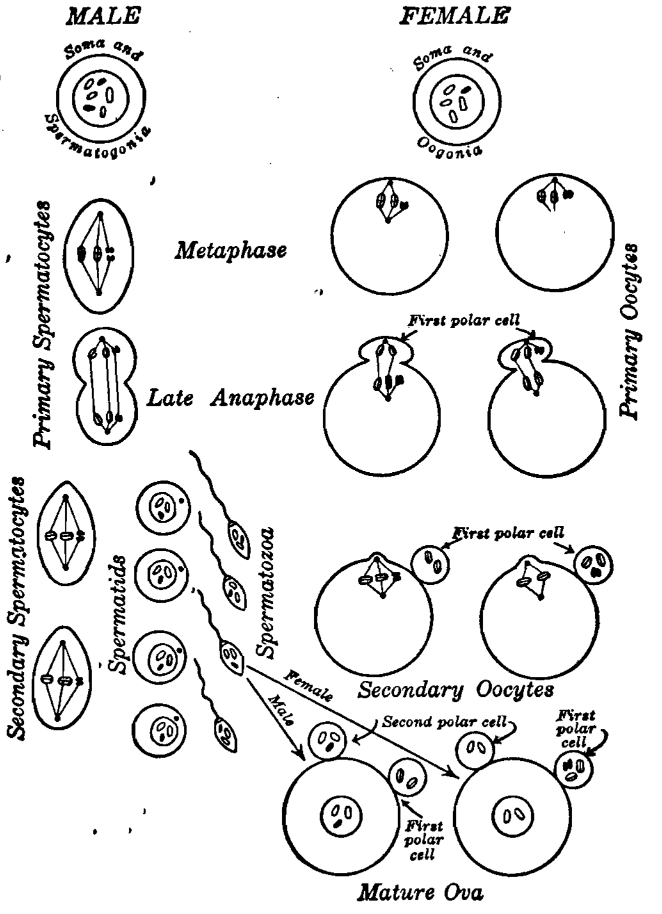

FIG. 83.—Sex determination in the case of heterogametic females.

and becoming fertilized, produces females, and another which, retaining the *z*-chromosome, produces males.

It is obvious that in this case (see Fig. 83), the sex

of the zygote depends entirely upon the *method of maturation of the ovum*, the retention or expulsion of the *z*-chromosome being the deciding factor in the determination of sex. If in any way maturation can be controlled by factors exerting an influence either from within the egg itself or external to it, then sex ratios may be altered from the normal 50 : 50. This has been done by Seiler in the case of moths by controlling the temperature of the developing ova at the critical time in the process of maturation.

The control of maturation offers a possible explanation of such sex ratios as have been obtained by Riddle in his forced breeding experiments on doves, where females are produced in the latter part of the breeding season from large eggs and males in the early part of the season from small eggs.

3. Sexual Cycles

A. APHIDS AND PHYLLOXERANS

Most enlightening observations on the determination of sex by means of influencing maturation, have been made upon aphids and phylloxerans by Morgan and by Von Baehr. It is well known that in the case of *Aphis* fertilized eggs always produce females. Under favorable conditions both males and females are produced parthenogenetically, the males, however, always arising from smaller eggs than the females.

It has been observed too that in these smaller eggs (Fig. 84) an entire *x*-chromosome is extruded in the giving off of the one polar cell, leaving in the egg

APHID-PHYLLOXERAN CHROMOSOME CYCLE

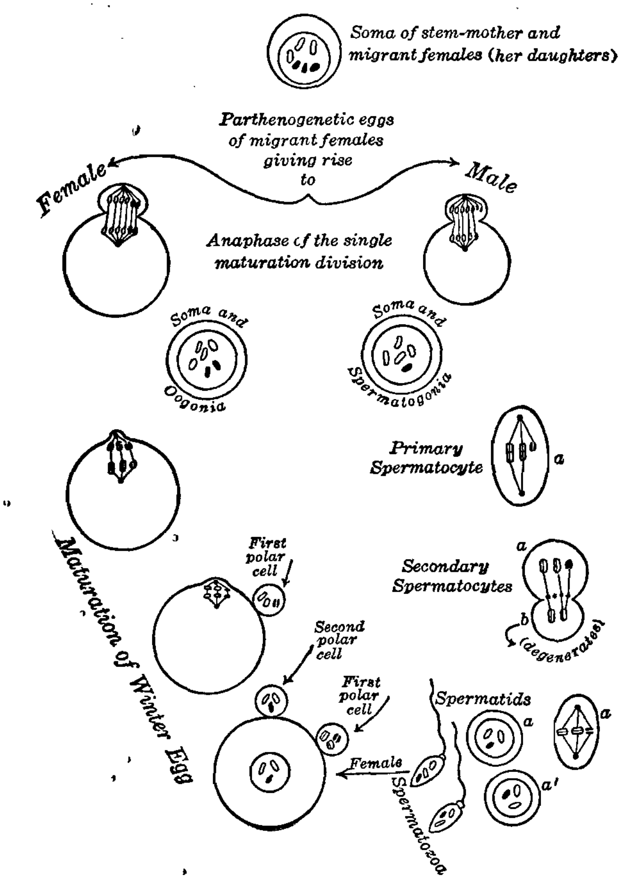

FIG. 84.—The chromosome cycle in parthenogenesis of aphids and phylloxerans.

$2n + x$ chromosomes (five in number) and that such an egg forms a male. On the other hand, in the larger

parthenogenic eggs no whole x-chromosome is extruded into the single polar cell given off and consequently the egg, retaining $2n + xx$ chromosomes (six in number), develops into a female.

In the spermatogenesis of these forms it has been found that only one secondary spermatocyte develops from each primary spermatocyte, namely, the one which receives the x-chromosome. Thus, only two instead of four spermatids result from a primary spermatocyte and these two form female-determining spermatozoa. The "winter eggs" of these insects have two maturation divisions reducing the chromosomes to the haploid condition. The female diploid number is restored upon fertilization.

It would seem, therefore, that in the phylloxerans and aphids at least, maturation is actually controlled by the size and composition of the egg.

B. ROTIFERS AND DAPHNIDS

It is unfortunate that the rotifers and daphnids, which lend themselves so favorably to breeding experiments, are not as favorable cytological material as the homopterons, for it is not at all unlikely that their sex-determination rests upon a similar basis to that above described.

In rotifers and daphnids, as in homopterons, fertilized eggs give rise to females, whereas during parthenogenesis both females and males may arise, the latter coming from smaller eggs than the former. These facts are all the more interesting for the reason

that Whitney and A. F. Shull, each working separately on rotifers, have been able, through modification of external conditions, to alter the normal cycle of reproduction, by causing the continuance of the parthenogenetic process beyond the normal limit.

It seems evident that, through the modification of external conditions, they have succeeded *in influencing the type of egg produced.* If this case is really parallel to that of *Aphis* and *Phylloxera*, then the type of egg artificially produced ought thereafter to control its own maturation.

In daphnids, where parthenogenesis alternates with the sexual cycle, at least three kinds of eggs are produced; (1) thick-shelled, fat-laden, ephippial eggs which must be fertilized in order to develop; (2) thin-shelled, glycogen-laden, parthenogenetic eggs, which develop into females without fertilization; and (3) thin-shelled, smaller, parthenogenetic eggs which develop into males. The type of egg produced, as shown by Smith, may be influenced by temperature and also by food. It is not improbable that we may yet discover in the maturation of these ova differences in chromosomal behavior correlated with each type of ovum and the sex of the resulting offspring.

C. THE HONEY BEE

Closely allied to the problem of the sex cycle, as described in experiments with the homopterons, is the question of sex-determination as observed in the *hymenoptera.*

Even before chromosomes were known, Dzierzon postulated that males of this group (drones) are formed from unfertilized eggs, and females (worker and queens) from fertilized eggs, a view which has been substantiated by both cytological and genetical observations. Newell has shown that in the cross between Italian (gray) queens and German (dark) drones, as well as in reciprocal crosses, the male offspring are purely maternal, while the females are hybrid in character. Cytological observations by Petrunkevitch and by Nachtsheim have also established the validity of the Dzierzon theory.

Coupled with this, studies on the spermatogenesis of *hymenoptera* have revealed the fact that the spermatogonia possess solely the haploid number of chromosomes, and in order, therefore, that this number be not further reduced in the process of maturation, only one division of chromatin takes place. In the first spermatocyte division of the honey bee all the chromatin passes to a single chromosome, only a minute degenerate non-chromatic globule being formed at the other pole of the spindle. In the second spermatocyte division the chromatin divides but one of the spermatids is very small and degenerates. Thus, instead of four spermatids, only one is formed and this one contains the haploid number of chromosomes.

Variations of this process are found in other *hymenoptera* which frequently result, in the formation from the larger second spermatocyte, of two separate spermatids each possessing the haploid number of chromosomes.

4. Polyembryony

Closely allied to the chromosomal basis of sex are the facts of polyembryony, for when more individuals than one are formed from a single ovum they are invariably of the same sex. Classical examples are parasitic *hymenoptera*, principally of the families *Proctotrypidæ* and *Chalcididæ*, in which thousands of individuals often result from a single egg. Other examples are the quadruplets formed in the nine-banded armadillo, *Tatusia,* and identical or monochorial twins in man and other mammals.

In the case of mammals the type of sperm, either with or without the x-chromosome, is undoubtedly the deciding factor in sex determination, for the reason that when all of the chromosomes of the zygote divide normally the sex of the resulting individuals must be the same. In other ways also they will be genetically identical.

In *hymenoptera* sex depends entirely upon whether fertilization or parthenogenesis takes place. A fertilized egg will result in females and an unfertilized one in males, a supposition based upon direct cytological observation. The facts of polyembryony thus offer strong substantiation to the idea of chromosomal determination of sex.

5. Sex-linked Inheritance

The association of Mendelian characters with particular chromosomes is nowhere better shown than in

the case of sex-linked characters, the genes for which are undoubtedly located in the sex-chromosomes, and whose inheritance follows exactly the distribution of these chromosomes. About thirty genes of this kind have been discovered in *Drosophila* alone. (See Fig. 76, the left hand line.)

Sex-linked inheritance, which means that genes for characters *other than sex* are associated with a particular sex, *i.e.*, are carried in the same chromosome that bears the sex-determining genes, should not be confused with *sex-limited* characters, *i.e.*, with secondary sexual characters that are found in one sex only but the genes for which may be located in any chromosome.

A. DROSOPHILA'S RED EYES

An example of a dominant sex-linked character is the red eye of *Drosophila*. The manner of its inheritance is as follows.

If a red-eyed female is mated with a white-eyed male (Fig. 85), the F_1 generation are all red-eyed, and when members of the F_1 generation are inbred the F_2 generation shows the expected proportion of three red-eyed individuals to one white-eyed. However, a peculiar result appears inasmuch as all of the white-eyed individuals are males. Thus, one half of the F_2 males are white-eyed like their grandfathers while all of the F_1 females are red-eyed because the character of white-eyes is covered up when the gene for red is present. The eggs of F_1 females, however, which eliminate the genes for red eyes in the polar body

during maturation and are then fertilized by a sperm bearing a *y*-chromosome, mature into white-eyed offspring.

The reciprocal cross of white-eyed females with red-

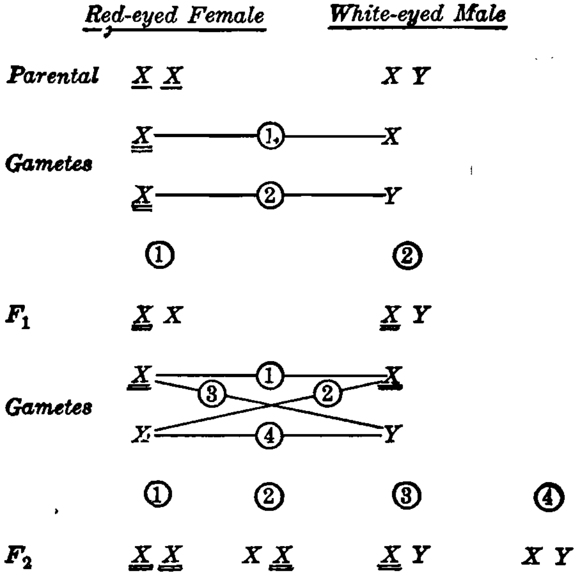

FIG. 85.—Criss-cross inheritance. The underscored *X* means the presence of the genes for red eyes in the sex-chromosome. The male is heterozygous.

eyed males, gives an entirely different result (Fig. 86.) It will be seen that in this case the F_1 females are red-eyed like their fathers, while the males are white-eyed like their mothers. In the F_2 generation half of the males and half of the females are white-eyed and the others are red-eyed, due to the fact that the male mechanism which has only one *x*-chromosome,

is capable of bearing the gene for red in only half of its germ-cells. The F_1 females, which normally carry two x-chromosomes, all receive an x-chromosome from their father and are consequently red-eyed, while the

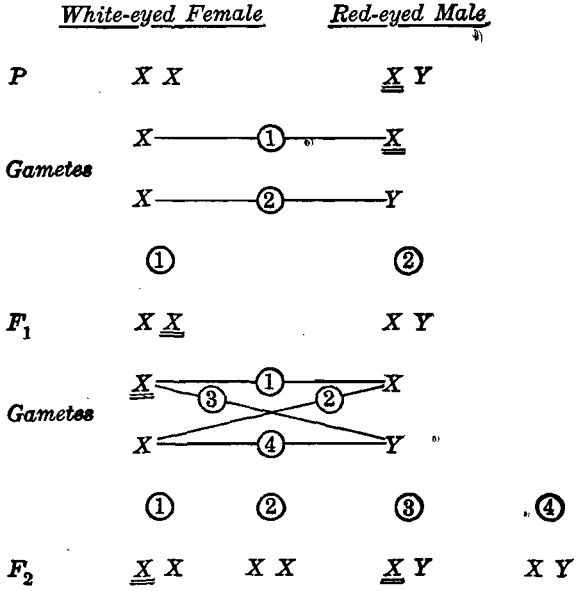

FIG. 86.—Criss-cross inheritance. The reciprocal cross to that shown in Fig. 85. All individuals with underscored *X* have red eyes. The male is heterozygous.

F_1 males all receive a single x-chromosome from their white-eyed mother and are, therefore, themselves white-eyed.

B. COLOR-BLINDNESS IN MAN

This criss-cross type of inheritance has long been known in man, color-blindness being perhaps the best

known example of a sex-linked character, behaving in its inheritance exactly as that of red-eye in *Drosophila.* That color-blind females are so rare is due to the fact that it requires a duplex, or homozygous, dose of the determiner for color-blindness to produce a color-blind female, while only a simplex, or heterozygous, dose is

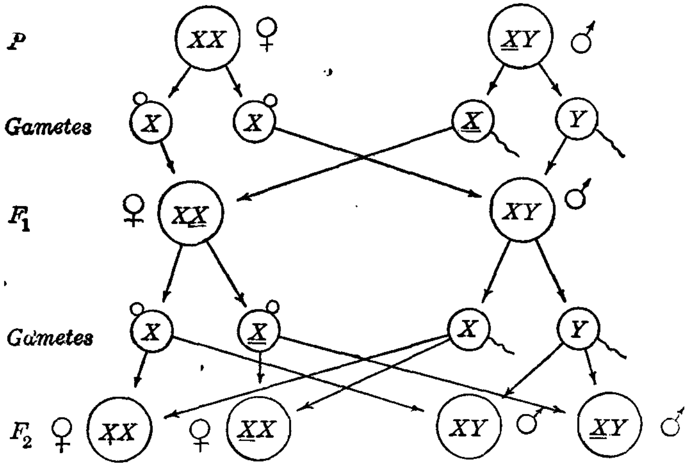

FIG. 87.—General diagram for sex-linked inheritance. The underscored symbol (X) represents a sex determiner with some other character (as color-blindness) linked with it.

needed to produce a color-blind male. These facts agree perfectly with the idea that the female is homozygous and the male heterozygous with respect to sex, and that the factor for color-blindness is linked with the determiner for sex. Sex-linked inheritance, as shown in this case, may be illustrated by the diagram above (Fig. 87) in which, for the sake of simplicity, only sex chromosomes and the determiners for color-

blindness are represented. Underscored $\underline{X}$ represents a color-blind determiner linked to a sex chromosome.

From this diagram, which agrees substantially with the facts, it is apparent that a color-blind male mated to a normal female will produce no color-blind offspring, although the females will be "carriers" of color-blindness, that is, will possess the factor in simplex form and will, therefore, carry it *for the female* in a latent condition.

Parents		Expected Offspring	
♂ Normal	♀ Color-blind	♂ Color-blind	♀ Carrier
Normal	Carrier	½ color-blind ½ normal	½ carrier ½ normal
Color-blind	Normal	Normal	Carrier
Color-blind	Color-blind	Color-blind	Color-blind
Color-blind	Carrier	½ color-blind ½ normal	½ color-blind ½ carrier

The sons of such a mating having a normal mother and a color-blind father will be absolutely free from the defect and cannot produce color-blindness in any of their offspring when mated with a normal strain. If, however, the "carrier" daughters from such a parentage, who are genotypically heterozygous for color-blindness but phenotypically normal, mate with normal individuals, the expectation is that one half of the sons, and none of the daughters will be color-blind, but that one half of these daughters will carry

the color-blind determiner in simplex form, that is, in a condition ineffective for producing color-blindness in female individuals.

All of the various possibilities in the inheritance of

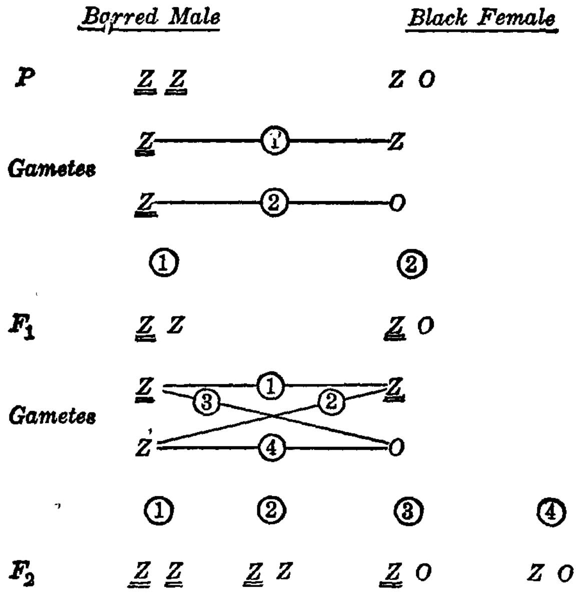

Fig. 88.—Sex-linked inheritance, with the female heterozygous. The "barred" character is indicated by underscored letters.

color-blindness according to the sex-linked interpretation are indicated in the table on page 282.

C. THE BARRED PLYMOUTH ROCK

In animals in which the female is heterogametic (*Lepidoptera* and birds) sex-linked characters are like-

wise known to exist and, in fact, were first discovered in moths by Doncaster. In these cases it is the female instead of the male that possesses the mechanism whereby the character in question can be present only once.

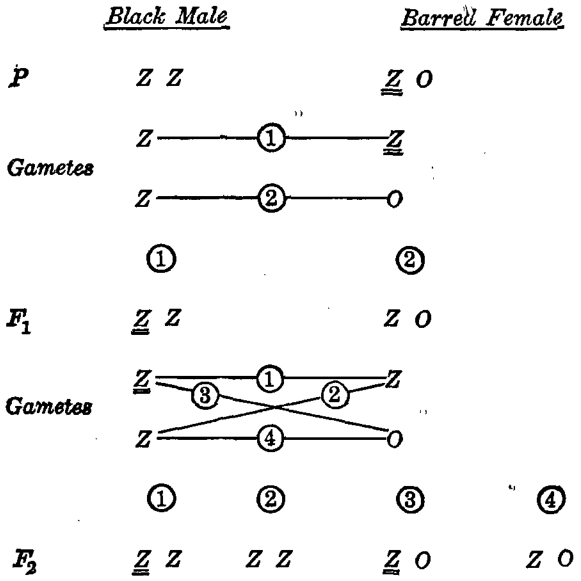

FIG. 89.—Sex-linked inheritance, with the female heterozygous. Reciprocal cross to that shown in Fig. 88. The "barred" character is indicated by the underscored gametes.

For example, "barring" is a dominant sex-linked trait in poultry, as shown in Figures 88 and 89.

In the cross shown in Figure 88 all the males and half the females in the F_2 generation are barred while in the reciprocal cross shown in Figure 89 the F_1 males are barred because they have a z-chromosome from their

maternal side, while the F_1 females are black because their single *x*-chromosomes came from their black father.

6. Non-disjunction

A striking confirmation of the chromosomal interpretation of sex is furnished by the phenomenon of *non-disjunction* discovered in 1913 by Bridges. In attempting to explain certain unexpected ratios which he obtained in a long series of breeding experiments upon white-eyed *Drosophilas*, Bridges found that his results would be more intelligible if what he termed "non-disjunction" was assumed to occur.

By non-disjunction is meant that both the *x*-chromosomes instead of disjoining and going normally to the two poles during the last maturation division, remain attached to each other and pass together to one pole leaving the other pole without any *x*-chromosome. In consequence, half the mature eggs should be provided with two *x*-chromosomes and half with none at all. Cytological examination of these unusual flies showed that this was what actually did sometimes happen.

The progeny of non-disjunctional white-eyed females, as shown in Figure 90 taken from Sharp's "Introduction to Cytology", show a theoretical diversity of characters which is borne out in the results of actual breeding. Morgan sums the matter up when he says:—"An abnormal distribution of sex-chromosomes goes hand in hand with an abnormal distribution of all sex-linked factors."

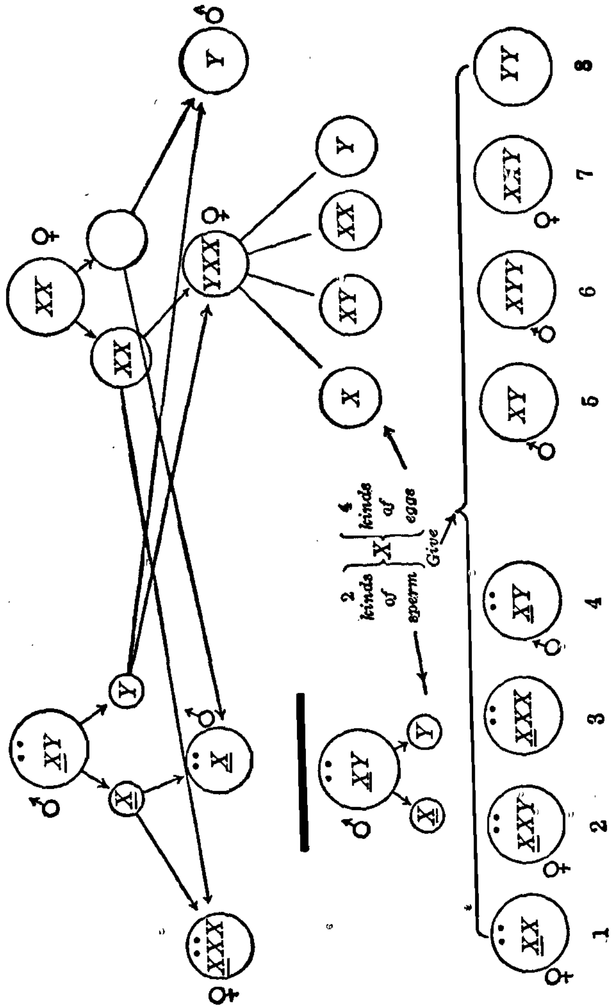

FIG. 90.—(For explanation see page 287).

Explanation to Figure 90

"Non-disjunction and its results in *Drosophila.* The two large circles in the first row represent male and female flies producing sperms and eggs respectively. Non-disjunction in the female gives 2 kinds of eggs, with *XX*- and no sex-chromosomes, instead of the normal single kind with one *X*. At fertilization there are possible 4 combinations rather than 2, as shown in the large circles of the second row. Owing to the several ways in which her 3 sex-chromosomes may be distributed at maturation, the female represented by the third circle produces 4 kinds of eggs. When mated to a normal male (below the horizontal line) with two kinds of sperms, 8 combinations are possible (last row). Numbers 1, 4 and 5 are normal flies and give the usual type of progeny. Numbers 2, 6 and 7, owing to the presence of 3 sex-chromosomes, give exceptional results when bred. Types Numbers 3 and 8 do not appear in the cultures, probably because they die very early. The original male has red eyes and the original female white eyes. Red eyes (represented by the dots) appear in every fly bearing the *X*-chromosome of the original male."

(Diagram by Sharp based on data from Bridges and Morgan.)

7. Secondary Sexual Characters and Hormones

It will be seen, from the preceding illustrations that the primary differences between the sexes is in the kind of gametes which they form. The female is an egg-producer, the male a sperm-producer. In many animals especially invertebrates, it is very difficult to distinguish males from females without first examining the gonads, although there is no lack of forms in which one can with ease distinguish the sexes solely by external appearances.

Very often this sexual dimorphism is confined, first, to the genitalia or to accessory apparatus used in copulation, oviposition, or rearing of the young; and second, to extra genital characteristics not associated directly with reproduction, such as color, ornamentation, and the like. Both of these types of sexual

dimorphism are, however, secondary to gamete production.

In mammals and birds these so-called secondary sexual characters are found to be largely dependent for their proper development upon the normal presence and activity of the gonads. For example, castration of young male mammals results in individuals lacking in many ways the attributes of normal males. Among cattle and horses, which have undergone this operation, the fiery males become docile and lack the thick neck common to their kind. They also put on fat more readily. In man the voice fails to change, the beard is weak, the epiphyses of the bones do not fuse and the spirit is dulled. Females deprived of ovaries early in life fail to develop normal mammary glands, while certain of their skeletal characters are likewise much altered. Extensive experiments have proved that in birds and mammals secretions of the gonads, known as *hormones*, are essential to normal development. The castration of young male rats followed by ingrafting of ovaries causes these individuals to become feminized in character.

Perhaps no better case of the influence of hormones is known than that of the "free martin," adequately explained by the observations of Lillie. He found in cattle that when the chorionic coverings of twin embryos of opposite sex fuse so that the blood vessels anastomose, the more rapidly developing male embryo sends out hormones into the circulation which inhibit the normal development of the female embryo. The much modified female embryo may then be born as a

free martin in which the ovaries tend to form tubules quite like those of a testis.

In birds the activities of the gonads likewise control to a large extent the development of the secondary sexual characters, as has well been shown by Goodale and by Morgan in castration and transplantation experiments on ducks and fowls. Most striking is the case of female birds which, when castrated while still young, develop male plumage and posture.

It has been clearly demonstrated that the genes for secondary sexual characters lie in the autosomes and thus both male and female have determiners for the secondary sexual characters of both sexes. For example, normally in cases where the male is heterogametic, the presence of a single x-chromosome in all of its cells, together with the endocrine secretion of its gonads, causes the male genes for secondary sexual characters to develop and those of the female to be suppressed. By castration and transplantation the normal condition may be upset and the female secondary sex genes brought into action.

The whole problem of sex-hormones is very complicated since it has been shown that the secretion from the gonads is merely one link in the chain of endocrine factors which tend to set into action the genes for determining secondary sexual characters. In the development of sex in the vertebrates the genes for the production of these sex-hormones are second in importance only to those genes which determine whether ova or sperm shall be formed in an individual.

8. The Effect of Parasitism on Sex

It has been well demonstrated in insects that castration, even of very young individuals, produces no effect upon the secondary sexual characters when the animal reaches its adult form. Even the implantation of gonads of the opposite sex results in no change. The growth and development of the soma seems to be fixed by the chromosomal complex and does not appear to be influenced by the action of any sex-hormone. Alterations of secondary sexual characters may occur, however, by means of parasitism, as shown by experiments on crustacea and insects.

Among crustacea the best case of this kind perhaps is that of the crab *Inachus*, the male of which, when parasitized by the cirripede *Sacculina*, as described by Smith, becomes similar to the normal female in the form of its claw, abdomen and abdominal appendages.

Among insects *Thelia bimaculata*, described by Kornhauser, is a good example. Parasitized males resemble females even to the minute structure of their chitinous integument. Such alterations are due, very likely, to an entire upset in the metabolism of the host, changing the internal environment so fundamentally that the genes for the male secondary sexual characters fail to find the conditions necessary for their expression in the developing soma.

9. Gynandromorphs and Sex Intergrades

In insects and crustacea abnormal individuals occasionally appear, presenting both male and female

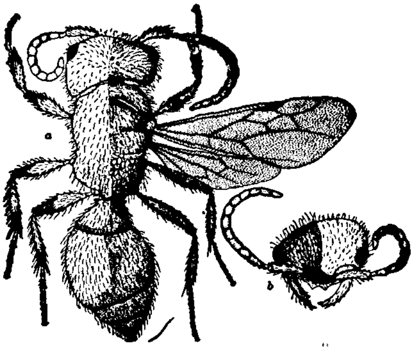

FIG. 91.—"A gynandromorph mutillid wasp, *Pseudomethoca canadensis,* male on right side, female on left." From Morgan's "Heredity and Sex," by permission of the Columbia University Press.

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characters. Sometimes the demarcation is exactly median, one-half being male and the other female. Such forms are true *gynandromorphs*. (Fig. 91.) There are cases, however, where the division may be either dorso-ventral or antero-posterior, and still others which show a patchwork of male and female parts, these latter being mosaic or inter-sex individuals. Examples of such sex-intergrades have been found among moths as described by Goldschmidt and by Banta among daphnids.

Insect gynandromorphs do not necessarily have the gonad of the corresponding sex in their respective halves, showing that the soma is not moulded by sex-hormones.

The cause of gynandromorphism has been studied by Boveri and by Morgan. Boveri claims to have found in gynandromorph bees of crossed races that the male half was maternal, and the female half hybrid. Obviously, if after the division of the egg-nucleus, a sperm unites with *one* of the daughter nuclei that half will be female, whereas the sister nucleus, developing parthenogenetically, will form a male half purely maternal in origin.

This explanation certainly holds good for some cases but Morgan finds in *Drosophila* that male portions of gynandromorphs often bear paternal characters, genes of which are in chromosomes other than the x-chromosome. He concludes, therefore, that at times an x-chromosome is lost during the meiosis of a female zygote, leaving a nucleus that fails to get two x-chromosomes, which, consequently, develops into the male portion of the gynandromorph.

Similarly a misplaced x-chromosome in a primary germ-cell may cause testes to form in a female. Such a case of gynandromorphism in *Thelia* (Kornhauser) proved upon actual chromosome count to have one x-chromosome missing.

It is rather difficult to offer any simple mechanical explanation for the mosaics or sex-intergrades of moths and daphnids. Goldschmidt has attempted to explain his results upon a quantitative basis, assigning values for the determiners for maleness and femaleness, and adding the assumption that the strength of these determiners varies in different races. Thus, the crossing of a strong male race with a weak male race brings about an upset of normal conditions, establishing a new balance of factors so that neither one sex nor the other predominates. An expression of two sets of genes, therefore, is brought about in various parts of the organism.

Bridges' recent work on triploid races of *Drosophila* seems to indicate that when the normal relation of the autosomal genes to the sex-genes of the x-chromosome is upset, either by the preponderance of one or the other, then sex abnormalities of many sorts may be expected.

10. Hermaphroditism

One of the most obscure problems of the entire sex question is that of hermaphroditism, or the production of ova and sperm by a single individual. Instances of this condition are found normally occurring in many groups of invertebrates, such as coelenterates, cteno-

phores, flat-worms, round-worms, annelids, molluscs and crustaceans. It is, however, the exception rather than the rule and must be viewed as a modification of the bisexual condition necessitated to insure insemination in animals poorly adapted to bring about typical fertilization of the eggs.

Sometimes hermaphrodites are female in appearance and again they resemble more closely the males of the group to which they belong. In certain Nematodes, for example, *Rhabdites aberrans*, an occasional male is found among thousands of hermaphrodites of female appearance. In this worm Miss Krueger has shown that occasionally there is a failure of one chromosome to become incorporated in one of the second spermatocytes. Spermatozoa resulting from such deficient spermatocytes may be the cause of these occasional male zygotes. Since our knowledge of the chromosomes in hermaphroditism is deficient, it is hardly worth while at present to speculate on the mechanism which produces such individuals.

That the sexual tendencies of hermaphroditic forms are often in a sensitive balance, influenced by external conditions, is shown by the experiments of Baltzer on *Bonellia* and by Gould on *Crepidula.*

In the marine worm *Bonellia* there are produced minute motile larvæ with hermaphroditic possibilities. If these free-swimming larvæ find the proboscis of a female *Bonellia* they attach themselves thereto and develop into minute males after a parasitic existence of about four days. If, however, no proboscis is encountered, the motile larva sinks to the bottom and develops

into a female. In this case we may say that some secretion from the female stimulates the development of the male potentialities and suppresses those of the female. In fact, intermediates were produced by Baltzer by allowing larvæ to become attached to a proboscis temporarily and then removing them at intervals of less than four days.

In *Crepidula plana*, a hermaphroditic gasteropod which is normally protandric, that is, producing first sperm and afterward ova, Gould has shown that the presence of older individuals during the female phase of development causes the production of sperm in such young individuals as, when isolated omit sperm production, developing instead the female phase and producing ova. Here there is an animal in sensitive balance influenced by a secretion which probably comes to it through the sea-water from individuals in the female phase of reproduction.

The problem of hermaphroditism, its mechanism and relationship to bisexual reproduction, is well worthy of intensive study. From such exceptions to the general rule we may hope to learn much about the normal mechanism of sex-determination.

11. Conclusion

Finally, one may ask, can sex ever be controlled? There seem to be two avenues of approach to this problem.

The maturation, and thereby sex, in forms in which the female is heterogametic, may be controlled by ex-

ternal conditions, as in the case of Seiler's moths and Riddle's doves. When, however, the male is heterogametic, it would be possible to control sex only by some agency which would differentially aid or inhibit the progress of one of the two kinds of sperm peculiar to this kind of an organism in its approach to, or penetration of, the ovum.

CHAPTER XIV

THE APPLICATION TO MAN

1. The Application of Genetics to Man

Human civilization goes hand in hand with the degree of successful interference which man exerts upon the natural forces surrounding him.

Primitive man was overwhelmed and outmastered by his environment, but civilized man harnesses nature to do his will. Savages are not proficient in the arts of cultivating plants and domesticating animals, while these are the very things upon which human progress fundamentally depends. The degree of civilization of any people is closely correlated with the degree of their success in exercising a conquering control over plants and animals. Any knowledge of the laws of heredity, therefore, as applied by man, either directly to himself or indirectly to animals and plants, is a distinct contribution to human progress.

In 1900 the National Association of British and Irish Millers, as Kellicott points out, being dissatisfied with the quality and quantity of the annual wheat yield, engaged Professor Biffen to apply his knowledge of heredity to the practical problem of improving their wheat crop. The characters desired were a short full head, beardlessness, high gluten content, immunity to

rust, strong supporting straw, and a large yield per acre. In the short time that has elapsed, Professor Biffen has succeeded in producing strains of wheat that combine all these desirable characters to a remarkable degree. Such an immediate result would not have been possible before 1900, when the rediscovery of Mendel's law revolutionized man's knowledge of the action of heredity in nature.

This same knowledge which has made possible the improvement of wheat may be applied with certain reservations to the breeding of man, for there is no reasonable doubt that man belongs in the same evolutionary series with all other animals, as Darwin showed, and is consequently subject to the same natural laws to a considerable degree.

It must be admitted that thus far in the progress of civilization more attention has been directed to the scientific breeding of animals and plants, little as that has been, than to the scientific breeding of man. Let us hope that the future will have a different story to tell!

2. Modifying Factors in the Case of Man

There are certain qualifying factors that make the problems of genetics somewhat different in the case of man than in other organisms.

For example, mankind has come to be partially exempt from some of the natural laws which affect other organisms. Thus with respect to the workings of *natural selection* man is partially under "grace" rather than "law." Nature no longer "selects" good eyes in

man by long, patient, and devious processes when poor eyes are made good almost instantly by a visit to the oculist. She has long since given up providing natural weapons of defense for those who have the wits to supply themselves more efficiently with artificial means of self-preservation, and she no longer attempts to improve the natural powers of locomotion of those who are able to tame a horse to ride upon, or who build steamships, railroads, automobiles and aeroplanes, thus accomplishing at once what would require ages at least to evolve.

Neither does the law of the *survival of the fittest* in its original sense apply equally to man and to other organisms. Human society to-day protects its unfit in hospitals, asylums, and through various philanthropies, while physicians devote themselves to the art of prolonging life beyond the period of usefulness.

We do not desire these results of our modern civilization to be otherwise, but the fact remains that some of the most inflexible and universal "natural laws" are ineffective in the case of man, and it is profitable to bear this in mind when applying the laws of genetics to man.

The laboratory for human heredity is the wide world, and it is obvious that the experimental method which has proven so effective in studying the heredity of animals and plants is impracticable in the case of man. The consideration of human heredity, therefore, must always be largely from the statistical side, consisting in an analysis of experiments already performed rather than in arbitrarily initiating new experiments.

Such institutions as insane asylums, prisons, sani-

tariums, and homes for the unfortunate are excellent foci for studying certain phases of human heredity, because they are simply convenient places where the results of similar dysgenic experiences have been brought together.

3. Experiments in Human Heredity

A. THE JUKES

A classic example of an experiment in human heredity which has been partially analyzed by the statistical method is that furnished by Dugdale in 1877 in the case of "Max Jukes" and his descendants. At that time it included over one thousand individuals, the origin of all of whom has been traced back to a shiftless, illiterate, and intemperate backwoodsman who started his experiment in heredity in western New York when it was yet an unsettled wilderness.

In 1877 the histories of 540 of this man's progeny were known, and that of most of the others was partly known. About one third of this degenerate strain died in infancy, 310 individuals were paupers who all together spent a total of 2300 years in almshouses, while 440 were physical wrecks. In addition to this, over one half of the female descendants were prostitutes, and 130 individuals were convicted criminals, including 7 murderers. Not one of the entire family had a common school education, although the children of other families in the same region found a way to educational advantages. Only 20 individuals learned a trade and 10 of these did so in state's prison.

It is estimated that up to 1877 this experiment in

human breeding had cost the state of New York over a million and a quarter dollars, not including the drink bill, and the end is by no means yet in sight.

The discovery in 1911 of Dugdale's original manuscript giving the real names and localities of the members of the Jukes clan made it possible to follow up the later history of this famous strain of undesirable human germplasm. This was done by Dr. A. H. Esterbrook, who published the results of his investigations under the title of "The Jukes in 1915,"[1] after personally visiting every individual whom he was able to trace.

Since Dugdale's time the Jukes, now in the eighth generation, have been forced to disperse from their original habitat because the cement mining industry upon which most of them formerly depended for a livelihood was abandoned with the introduction of Portland cement. Esterbrook has recorded 2094 individuals bearing Jukes' blood who were scattered through fourteen states. Of 748 living descendants of Max Jukes over 15 years of age, he found 76 who were socially adequate; 255 doing fairly well; 323 "typical degenerates," and 94 whom he left unclassified due to lack of sufficient information. He says:—"The removal of Jukes from their original habitat to new regions is beneficial to the stock *itself*, as better social pressure is brought to bear on them and there is a chance for mating into better families," and Davenport, commenting on the entire matter, adds,—"The most important conclusion that may be drawn from

[1] Carnegie Institution of Washington, Pub. 240, 1916, pp. 85.

Dr. Esterbrook's prolonged study of the Jukes forty years later is that not merely institutional care nor better environment will cause good social reactions in persons who are feeble-minded or feebly-inhibited, although on the other hand, better stimuli will secure better reactions from weak stock than will poor stimuli. . . . The chief value of a detailed study of this sort lies in this: that it demonstrates again the importance of the factor of heredity."

B. THE DESCENDANTS OF JONATHAN EDWARDS

In striking contrast to the case of Max Jukes is that of Jonathan Edwards, the eminent divine, whose famous progeny Winship describes as follows: "1394 of his descendants were identified in 1900, of whom 295 were college graduates; 13 presidents of our greatest colleges, besides many principals of other important educational institutions; 60 physicians, many of whom were eminent; 100 and more clergymen, missionaries, or theological professors; 75 were officers in the army and navy; 60 were prominent authors and writers, by whom 135 books of merit were written and published and 18 important periodicals edited; 33 American states and several foreign countries and 92 American cities and many foreign cities have profited by the beneficent influence of their eminent activity; 100 and more were lawyers, of whom one was our most eminent professor of law; 30 were judges; 80 held public office, of whom one was vice-president of the United States; 3 were United States senators; several

were governors, Members of Congress, framers of state constitutions, mayors of cities, and ministers to foreign courts; one was president of the Pacific Mail Steamship Company; 15 railroads, many banks, insurance companies, and large industrial enterprises have been indebted to their management. Almost if not every department of social progress and of public weal has felt the impulse of this healthy, long-lived family. It is not known that any one of them was ever convicted of crime."

Similarly Galton, in "Hereditary Genius," points out in his analysis of one hundred celebrated persons that they had 3 great-grandfathers; 17 grandfathers; 31 fathers; 48 sons; 14 grandsons and 3 cousins who also were celebrated.

C. THE KALLIKAK FAMILY

A more convincing experiment in human heredity than the foregoing, since it concerns the descendants of two mothers and the same father, is furnished by the recently published history of the "Kallikak" family.[1]

During Revolutionary days, the first Martin Kallikak,—the name is fictitious,—who was descended from a long line of good English ancestry, took advantage of a feeble-minded girl. The result of their indulgence was a feeble-minded son who became the progenitor of 480 known descendants of whom 143 were distinctly feeble-minded, while most of the others fell below mediocrity without a single instance of exceptional ability.

[1] "The Kallikak Family." H. H. Goddard. The Macmillan Co.

"After the Revolutionary war, Martin married a Quaker girl of good ancestry and settled down to live a respectable life after the traditions of his forefathers. From this legal union with a normal woman there have been 496 descendants. All of these except two have been of normal mentality and these two were not feeble-minded. . . . The fact that the descendants of both the normal and the feeble-minded mother have been traced and studied in every conceivable environment, and that the respective strains have always been true to type, tends to confirm the belief that heredity has been the determining factor in the formation of their respective characters."

Other recent extensive studies of dysgenic lines include the "Nams," the "Hill Folk," the "Pineys" of New Jersey, the "Ishmaels" of Indiana and the "Zeros" of Denmark.

4. Moral and Mental Characters behave like Physical Ones

These instances of human breeding show unmistakably that "blood counts" in human inheritance, even though the hereditary unit characters that lead to these general results have not yet been analyzed with the clearness that is possible in dealing with the characters of some animals and plants.

There is of course no question of moral and mental traits in plants, and the rôle that these play in animals is not easy to determine; but in man the case is undoubtedly much more important and complex, since

mental and moral characteristics have a large share in making man what he is. The brute acts according to his inherited organization; man is *urged* by his but *may* act according to a higher, moral law. There is, however, no fundamental scientific distinction which can be drawn between moral, mental, and physical traits, and they are undoubtedly all equally subject to the laws of heredity.

For instance, as an illustration of the heritability of non-physical traits, in the Jukes pedigree three of the daughters of Max impressed their peculiar moral and mental characteristics in a distinctive way upon their offspring. To quote Davenport: "Thus in the same environment, the descendants of the illegitimate son of Ada are prevailingly *criminal;* the progeny of Belle are *sexually immoral;* and the offspring of Effie are *paupers*. The difference in the germplasm determines the difference in the prevailing trait." As Woods observes: "The most interesting and even startling thing has been the ease with which heredity has been able to bear the brunt of explaining the general make-up of character."

5. The Character of Human Traits

Of the mental, moral, and physical traits which are heritable in man, some must be regarded as generally desirable, some as indifferent, and others as defects to be avoided if possible. In general the majority of human traits, those which together make up man as distinguished from other animals, do not particularly

claim the attention because they are so universal. Some which stand out from the mass, such as the physical traits of eye-color and the color and character of hair, may be regarded as indifferent so far as the welfare of the individual is concerned, while others like skin color and certain racial features that characterize particular strains of "blood" may, under certain circumstances, work a social handicap upon their possessors according to the traditions of the community in which they appear.

A long list of desirable mental traits might be enumerated that seem in a general way to be subject to the laws of inheritance, although they have not yet undergone the careful analysis demanded by modern genetics which deals in unit characters rather than in lump inheritance.

Musical, literary, or artistic ability, for example, mathematical aptitude and inventive genius, as well as a cheerful disposition or a strong moral sense are probably all gifts that come in the germplasm. They may each be developed by exercise or repressed by want of opportunity, nevertheless they are fundamentally germinal gifts.

A genius must be born of potential germplasm. There are no "self-made men." Each has within from his ancestry, the potentiality of whatever he becomes. No amount of faithful plodding application can compensate for a lack of the divine hereditary spark at the start.

6. Hereditary Defects

Undesirable hereditary traits are frequently defects due to the absence of some character. For instance, albinism, which occurs in several kinds of animals and also in man in one out of every 20,000 individuals (according to Elderton), is due to the absence of pigment in the skin, hair and eyes. Albinic individuals have poor eyesight because they are unable to stand strong light, being without protective pigment in the eyes. This peculiarity of albinism behaves as a recessive character both in man and in other animals. An albinic individual may, therefore, marry a normal individual without fear of producing albino children, although the children of such a mating would carry heterozygous germplasm with respect to albinism, and in cousin marriages might subsequently produce some albino children.

Davenport, in his work on "Heredity in Relation to Eugenics," brings together a long catalogue of human hereditary defects, although in most instances they are extremely difficult of accurate analysis. This is true, first, because these defects so often probably depend upon a combination of determiners rather than upon a single one, and, second, because the available data are usually scattered and incomplete.

Deafness, for example, is a defect which is hereditary though exactly to what degree, it is at present impossible to state. The following table taken from the extensive work of Fay (1898) upon "Marriage of the Deaf in America" gives some idea of the results of different matings lumped together statistically.

Condition of Parents	Percentage of Deaf Offspring
Both born deaf	25.9
One born deaf, one with acquired deafness .	6.5
One born deaf, one normal	11.9
Both with acquired deafness	2.3
One with acquired deafness, one normal . .	2.2

That two parents born deaf do not produce more than 26 per cent of deaf children is probably due to the fact, first, that each parent is in all likelihood heterozygous for deafness and that, second, the same combination of factors which is the cause of the parental defect on either side of the pedigree does not happen to recombine after segregation to form the new individual. Deafness will be produced in the offspring only when matings occur in which the proper factors are combined. Such an undesirable result is much more likely to happen if both parents come from the same, or related, hereditary strains than if they are derived from families in no way connected by blood.

Herein lies the biological objection to cousin marriage which tends to bring together, and thus to perpetuate, like defects. Outcrossing, on the contrary, through the law of dominance, tends to conceal defects and to prevent their expression.

If the patent parental characters were all that reappeared in the offspring, the marriage of near kin would present fewer difficulties. It is the "skeleton in the closet" that makes trouble. Elderton gives a case of hæmophilia where the direct line was free from taint

but collaterals showed the disease latent for six generations.

Inbreeding is often the result of proximity. Insular or isolated communities, slums in cities, where those of one language herd together, or hovels in the backwoods, where degenerates of a kind are kept in intimate association, as well as asylums of various sorts in which similar defectives are promiscuously housed under the same roof, are all-potent agencies to insure human inbreeding.

Similarly, localities which have been devastated by migrations of the most effective blood, as, for example, parts of Ireland or many rural villages in New England, are frequently characterized by a population showing a large percentage of defectiveness. The able-bodied and ambitious go forth into the world to seek their fortunes, while the deficient in body or spirit are left behind where, under the spell of proximity, they perpetuate their deficiencies.

The part that improved transportation has played in mixing up populations and in counteracting the effects of stagnation on human heredity, through inbreeding under the inertia of proximity, is very great. There were, obviously, geographic reasons for the well-known love story of Adam and Eve. Before the days of railroads, cousin-marriages were much more frequent than they are now.

Many cases of human defects, such as imbecility or insanity, are extremely difficult of analysis from the standpoint of heredity because, in the first place, the defective conditions descriptively included under these

vague terms are made up of a multitude of diverse conditions each of which must have a different array of determiners and, in the second place, because any one definite sort of insanity or imbecility may be conditioned by a variety of factors.

However, the difficulty of the problem is no reason for abandoning the attempt to reach its solution and to learn, if possible, "whence come our 300,000 insane and feeble-minded, our 160,000 blind or deaf, the 2,000,000 that are annually cared for by our hospitals and homes, our 80,000 prisoners and the thousands of criminals that are not in prison, and our 100,000 paupers in almshouses and out" (Davenport).

7. The Control of Defects

The method of possible control of human defects depends upon whether they are positive or negative, that is, dominant or recessive. In those cases where a given defect is due to a single determiner the Mendelian expectation for the possible offspring arising from various matings is indicated in the table on page 310 in which *D* stands for the defect and *d* for its absence.

If the defect is positive and in a duplex or homozygous condition in one parent, as in 1, 2, and 4 all the offspring will possess it regardless of the germinal constitution of the other parent. In two cases only, namely, in 3 and 5, where the defective parent is heterozygous, is there any chance of unaffected offspring, and even in these cases the defect is quite as

THE MENDELIAN EXPECTATION FOR DEFECTS

		If the Defect is Positive (dominant)	If the Defect is Negative (recessive)
When both parents show the defect	1	$DD \times DD =$ all DD	$dd \times dd =$ all dd
	2	$DD \times Dd = \frac{1}{2}DD + \frac{1}{2}Dd$	
	3	$Dd \times Dd = \frac{1}{4}DD + \frac{1}{2}Dd + \frac{1}{4}dd$	
When one parent only shows the defect	4	$DD \times dd =$ all Dd	$dd \times DD =$ all Dd
	5	$Dd \times dd = \frac{1}{2}Dd + \frac{1}{2}dd$	$dd \times Dd = \frac{1}{2}Dd + \frac{1}{2}dd$
When neither parent shows the defect	6	$dd \times dd =$ all dd	$DD \times DD =$ all DD
	7		$Dd \times DD = \frac{1}{2}DD + \frac{1}{2}Dd$
	8		$Dd \times Dd = \frac{1}{4}DD + \frac{1}{2}Dd + \frac{1}{4}dd$

likely to appear as not. It is obvious that the only way to rid germplasm of a dominant defect is by continued mating with recessive individuals. By this method it is possible in time to shake off the defect. When it once disappears in any individual, *it will never return* unless crossed back to a similar defective dominant strain.

In other words, such a recessive extracted from a heterozygous ancestry will breed just as true as a recessive which was pure from the start. In both instances there is an entire absence of the character in question, and it is clear that this character can thereafter never again reappear, since something cannot be derived from nothing.

On the other hand, if a defect is negative, depending upon the absence of a normal dominant determiner, as is usually the case with defects, it behaves as a Mendelian recessive, that is, it is always apparent in individuals developing from the homozygously defective germplasm.

It is certain, for example, that an imbecile which has arisen from homozygous defective germplasm carries only the determiner for imbecility in his own germplasm, and when two such recessives mate, nothing but imbecile offspring can result, for recessives breed true. Nothing plus nothing equals nothing.

For practical purposes it is unimportant to know

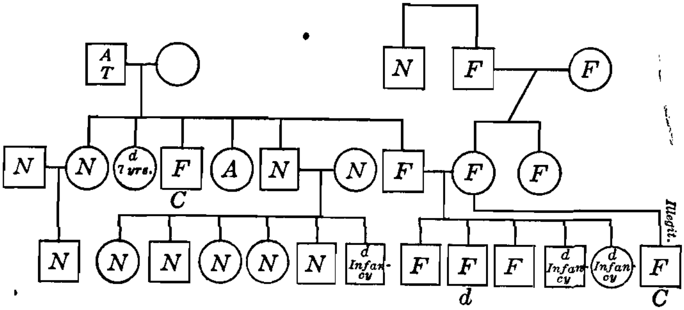

FIG. 92.—Pedigree chart illustrating the law that two defective parents have only defective offspring. *A*, alcoholic; *C*, criminalistic; *d*, died; *F*, feeble-minded; *T*, tubercular. After Goddard.

whether or not feeble-mindedness, or any similar defect, is Mendelian in behavior. The fact that it is hereditary is enough.

An illustration of this principle is given in the above pedigree (Fig. 92) furnished by Goddard, 1910. The result is quite different, however, when one parent only shows the defect. If the other parent is a normal homozygote, as in Case 4 of the accompanying table, all the offspring will be normal in appearance, but with the bar sinister of defectiveness in their germplasm, while if it is heterozygous (Case 5), one half of the progeny will be defective.

Finally, when neither parent shows defectiveness but one carries the defect as a heterozygote (Case 7), then there will be no defective children, while if both parents are heterozygous there is one chance in four that the offspring will be defective.

As a matter of fact, defectives usually mate with defectives for the simple reason that normals ordinarily avoid them, so it comes about that streams of poor germplasm naturally flowing together tend to the inbreeding of like defects.

Davenport[1] lays down the following general eugenic rules for the guidance of those who would produce offspring wisely: "If the negative character is, as in polydactylism and night-blindness, the *normal* character, then normals should marry normals, and they may be even cousins. If the negative character is *abnormal*, as imbecility and liability to respiratory diseases, then the marriage of two abnormals means probably all children abnormal; the marriage of two normals from defective strains means about one quarter of the children abnormal; but the marriage of a normal of the defective strain with one of a normal strain will probably lead to strong children. The worst possible marriage in this class of cases is that of cousins from the defective strain, especially if one or both have the defect. In a word, the consanguineous marriage of persons one or both of whom have the same undesirable defect, is highly unfit, and the marriage of even unrelated persons who both belong to strains

[1] Davenport. *Rep. of Amer. Breeders' Assoc.*, Vol. VI, p. 431, 1910.

containing the same undesirable defect is unfit. Weakness in any characteristic must be mated with strength in that characteristic; and strength may be mated with weakness."

In short, the eugenical Cupid does not tell one so often whom to select for a partner as whom to avoid.

CHAPTER XV

HUMAN CONSERVATION

1. How Mankind may be Improved

There are two fundamental ways to bring about human betterment, namely, by improving the individual and by improving the race. The first method consists in making the best of whatever heritage has been received by placing the individual in the most favorable environment and developing his capacities to the utmost through education. Such enterprises may be included under this head as improving sanitation, controlling disease, insuring health, safe-guarding human life, banishing child-labor, lessening drudgery of all kinds, substituting something better for the slums, championing the weak, reforming penal institutions, maintaining charitable organizations, cultivating true temperance, dispelling ignorance and lengthening life. The second method consists in seeking a better heritage with which to begin the life of the individual.

The first method is immediate and urgent for the present generation. The second method is concerned with ideals for the future, and consequently does not usually present so strong an appeal to the individual.

The first is the method of *euthenics*, or the science of learning to live well. The second is *eugenics*, which Galton defines as "the science of being well born." Every gain in eugenics, it need hardly be said, will make euthenics more effective but the reverse cannot be affirmed.

These two aspects of human betterment, however, are inseparable. Any hereditary characteristic must be regarded, not as an independent entity, but as *a reaction between the germplasm and its environment.* The biologist who disregards the fields of educational endeavor and environmental influence, is equally at fault with the sociologist who fails sufficiently to realize the fundamental importance of the germplasm.

Without euthenic opportunity the best of heritages would never fully come to its own. Without the eugenic foundation the best opportunity fails of accomplishment. The euthenic point of view, however, must not distract the attention now, for the present chapter is particularly concerned with the program of eugenics.

2. Human Assets and Liabilities

In an attempt to take account of human stock Dr. H. H. Laughlin, of the Eugenics Record Office, has made the following eugenical classification based on the manner in which families assemble in their offspring heritable traits which determine for their possessors (*a*) social adjustment and (*b*) special talent or defect.

I. Persons of genius;
II. Persons of special skill, intelligence, courage, unselfishness, enterprise or strength;
III. Persons constituting the great normal middle class, the "people";
IV. Socially inadequate persons.

The first three groups constitute those eugenically fit from sterling inheritance, who produce the socially valuable nine-tenths of humanity among civilized people, and in the last group are the eugenically unfit from defective inheritance who produce the socially inadequate or the "submerged tenth" of humanity.

Among persons of genius Dr. Laughlin would include the 5000 persons most splendidly equipped by nature throughout historic times, as, for example, Aristotle in philosophy, Newton in science, Pasteur in medicine, Dante in poetry, Shakespeare in drama, and Cecil Rhodes in business. Reckoning that since civilization began there have been born and reared in civilized countries approximately thirty billion persons, the expectation of a genius is about 1 : 6,000,000.

In the second group are included the "natural and acknowledged leaders in all lines of human endeavor,—the "*Who's Who* people." The incidence of these in the total population is possibly 1 : 6,000.

The third group, the "people," constitute nine-tenths of all, since the first two classes, although their influence is very great, are numerically negligible, while the fourth group is made up of the residue or the socially inadequate, namely, (1) feeble-minded; (2)

pauper; (3) inebriate; (4) criminalistic; (5) epileptic; (6) insane; (7) asthenic or weak; (8) diathetic, or predisposed to disease; (9) deformed; (10) cacæsthenic, that is, with defective sense organs.

Laughlin concludes;—"The task of eugenics is (1) to encourage fit and fertile matings among those persons most richly endowed by nature and (2) to devise practicable means for cutting off the inheritance lines of persons of naturally meagre or defective inheritance."

3. More Facts Needed

Since the point of attack in human heredity must be largely statistical, it is of the first importance to collect more facts. Our actual knowledge is confused with a mass of tradition and opinion, much of which rests upon questionable foundations. The great present need is to learn more facts; to sift the truth from error in what is already known; and to reduce all these data to workable scientific form. Much progress is being made in this direction, owing to the impetus given by the revival of Mendel's illuminating work, but as yet the science of eugenics is in its infancy.

Eugenics, being a biological science, its truths cannot be arrived at by arbitration and discussion, and no doubt the entire eugenic movement has suffered much at the hands of its over-enthusiastic friends. There is a wide difference between eugenic zeal and eugenic knowledge and wisdom.

"If there is one thing to be deprecated little less than ignorance or indifference," says Sir John MacDonald,

"it is science in a hurry,—eagerness to go to market with one's crops before they are fully ripe."

The most systematic and effective attempt in this country to collect reliable data concerning heredity in man has been initiated under the leadership of Dr. C. B. Davenport in connection with what is now the Department of Genetics of the Carnegie Institution of Washington. This began in 1910 as the Eugenics Record Office, with a staff of expert field and office workers and an adequate equipment of fire-proof vaults, etc., for the preservation of records, at Cold Spring Harbor, Long Island, New York, under Dr. H. H. Laughlin as superintendent. "The main work of this office is investigation into the laws of inheritance of traits in human beings and their application to eugenics. It proffers its services free of charge to persons seeking advice as to the consequences of proposed marriage matings. In a word, it is devoted to the advancement of the science and practice of eugenics." Already a considerable number of publications have been issued from the Eugenics Record Office.

The Volta Bureau, founded about thirty-five years ago in Washington by Dr. Alexander Graham Bell, is collecting data with reference to deafness and has now systematically arranged particulars concerning the history of over 20,000 individuals. In England, also, the Galton Laboratory for Eugenics, founded in 1905, is systematically collecting facts about human pedigrees and publishing the results in a compendious "Treasury of Human Inheritance."

Besides these special bureaus of investigation, innumerable facts about the inheritance of particular traits are being incidentally brought together and made available in various institutions and asylums throughout the world immediately concerned with the care of defectives of different types. It is in connection with such institutions for defectives that much of the most successful "field work" is being accomplished in the United States.

4. Further Application of What we know Necessary

Human performance always lags behind human knowledge. Many persons who are fully aware of the right procedure do not put their knowledge into practice. It follows, therefore, that any program of eugenics which does not grip the imagination of the common people in such a way as to become an effective part of their very lives is bound to remain largely an academic affair for Utopians to quarrel and theorize over.

It is not enough to collect facts and work out an analysis and interpretation of them, for, important as this preliminary step is, it must be followed by a convincing campaign of education.

The lives of the unborn do not force themselves upon the average man or woman with the same insistency as lives already begun. In the midst of the overwhelming demands of the present, the appeal of posterity for better blood is vague and remote. If

every individual regarded the germplasm he carries as a sacred trust, then it would be the part of an awakened eugenic conscience to restrain that germplasm when it is known to be defective or, when it is not defective, to hand it on to posterity with at least as much foresight as is exercised in breeding domestic animals and cultivated plants.

The eugenic conscience is in need of development, and it is only when it becomes thoroughly aroused in the rank and file of society as well as among the leaders, that a permanent and increasing betterment of mankind can be expected.

5. Restriction of Undesirable Germplasm

A negative way to bring about better blood in the world is to follow the clarion call of Davenport and "dry up the streams that feed the torrent of defective and degenerate protoplasm."

The education of the feeble-minded, the cure of the insane and the reform of the criminal are all euthenic not eugenic means of relief. Some idea of the extent of the drag of the "submerged tenth" upon human society may be gained from the following table, the data for which are derived from the U. S. census.[1]

The burden of the three undesirable D's, "defectives, dependents and delinquents," upon human society is by no means entirely represented in the dollar-column of this table. Each individual recorded is a human being, the member of some family and community,

[1] Statistical Directory of State Institutions for the Defective, Dependent and Delinquent Classes. Washington, 1919.

State Institutions for Defective, Dependent and Delinquent Classes

Institutions for	No. of Inmates Jan. 1, 1916	No. of Institu-tions	Expenditures for maintenance and operation in 1915
1. Insane	199,340	147	$36,312,662.20
2. Criminalistic	95,985	170	21,244,892.00
3. Dependent	45,373	84	9,675,932.37
4. Tuberculous	7,187	45	3,539,454.95
5. Feeble-minded	19,298	27	3,341,442.85
6. Deaf	6,826	33	1,893,490.09
7. Epileptic	6,097	9	1,345,821.57
8. Feeble-minded and epileptic	6,984	9	1,285,500.05
9. Blind	3,118	28	1,066,973.14
10. Blind and deaf	2,233	12	615,468.41
11. Inebriate	615	3	232,080.62
12. Deformed	601	4	206,747.23
13. Criminalistic and dependent	814	1	105,705.86
14. Feeble-minded, blind and deaf	191	1	67,051.73
15. Blind, deaf and dependent	215	1	59,649.67
16. Leprous	114	2	56,118.19
Total	394,991	576	$81,048,990.93

which must be more or less directly borne down by the unfortunate one. Moreover, the unfortunates who are in institutions are but a small percentage of the total number in the population who are not in institutions. It should be remembered that although heredity plays an important part in such life-tragedies it is not entirely to blame for these depressing data.

The restriction of undesirable additions to our human stock may be partially accomplished, at least in America, by employing the following agencies:—control of immigration; more discriminating marriage

laws; a quickened eugenic sentiment; sexual segregation of defectives; and finally, drastic measures of asexualization when necessary. Providing for the eugenic elimination of defectives is as truly a civic duty as administering charity to them after they are born.

A. CONTROL OF IMMIGRATION

The enforcement of immigration laws tends to debar from the United States not only many undesirable individuals, but also incidentally to keep out much potentially bad germplasm that, if admitted, might play havoc with future generations.

For example, during the year of 1908, 65 idiots, 121 feeble-minded, 184 insane, 3741 paupers, 2900 individuals having contagious diseases, 53 tuberculous individuals, 136 criminals, and 124 prostitutes were caught in the sieve at Ellis Island alone and turned back from this country by the immigration officials in spite of the fact that an average of only 8 cents a head was expended upon inspection.

These 7000 and more individuals probably were the bearers of very little germplasm that we are nationally not better off without.

Eugenically, the weak point in the present application of immigration laws is that criteria for exclusion are phenotypic in nature rather than genotypic, and consequently much bad germplasm comes through our gates hidden from the view of inspectors because the bearers are heterozygous, wearing a cloak of desirability over undesirable traits.

It is not enough to lift the eyelid of a prospective parent of American citizens to discover whether he has some kind of an eye-disease or to count the contents of his purse to see if he can pay his own way. The official ought to know if eye-disease runs in the immigrant's family and whether he comes from a race of people which, through chronic shiftlessness or lack of initiative, have always carried light purses.

In selecting horses for a stock-farm an expert horseman might rely to a considerable extent upon his judgment of horseflesh based upon inspection alone, but the wise breeder does more than take the chances of an ordinary horse-trader. He wants to be assured of the *pedigree* of his prospective stock. It is to be hoped that the time will come when we, as a nation, will rise above the hazardous methods of the horse trader in selecting from the foreign applicants who knock at our portals, and that we will exercise a more fundamental discrimination than such a haphazard method affords, by demanding a knowledge of the germ-plasm of these candidates for citizenship, as displayed in their pedigrees.

This may possibly be accomplished by having trained inspectors located abroad in the communities from which our immigrants come, whose duty it shall be to look up the ancestry of prospective applicants and to stamp desirable ones with approval.

This should be done by our own government and not by labor contractors or steamship companies who are not actuated by any eugenic considerations. Moreover, any immigration law requiring certificates from

foreign governments would seriously interfere with our getting many desirable foreigners to come to this country.

The national expense of such a program of genealogical inspection would be far less than the maintenance of introduced defectives, in fact it would greatly decrease the number of defectives in the country. At the present time this country is spending over one hundred million dollars a year on defectives alone, and each year sees this amount increased.

The United States Department of Agriculture already has field agents scouring every land for desirable animals and plants to introduce into this country, as well as stringent laws to prevent the importation of dangerous weeds, parasites, and organisms of various kinds. Is the inspection and supervision of human blood less important?

B. MORE DISCRIMINATING MARRIAGE LAWS

Every people, including even the more primitive races, make customs or laws that tend to regulate marriage. Of these, the laws which relate to the eugenic aspect of marriage are the only ones that concern us in this connection. "Marriage," says Davenport, "can be looked at from many points of view. In novels as the climax of human courtship; in law largely as two lines of property descent; in society, as fixing a certain status; but in eugenics, which considers its biological aspect, marriage is an experiment in breeding."

Certain of the United States have laws forbidding the marriage of epileptics, habitual drunkards, paupers, idiots, the insane, feeble-minded, and those afflicted with venereal diseases. It would be well if such laws were not only more uniform and widespread, but also more rigidly enforced.

The fact that much marriage taboo already exists regardless of laws which effectually hinder or prevent certain kinds of undesirable matings, forms a basis of hope for future control.

It is quite true that marriage laws in themselves do not necessarily control human reproduction, for illegitimacy is a factor that must always be reckoned with; nevertheless such laws do have an important influence in regulating marriage and consequent reproduction.

Marriage laws may, however, sometimes bring about a deplorable result eugenically, as in the case of forced marriage of sexual offenders in order to legalize the offense and "save the woman's honor." To compel, under the guise of legality, two defective streams of germplasm to combine repeatedly and thereby result in defective offspring just because the unfortunate event happened once illegitimately, is fundamentally a mistake. Darwin says: "Except in the case of man himself hardly any one is so ignorant as to allow his worst animals to breed."

C. AN EDUCATED SENTIMENT

A far more effective means of restricting bad germplasm than placing elaborate marriage laws upon our

statute-books is to educate public sentiment and to foster a popular eugenic conscience, in the absence of which the safeguards of the law must forever be largely without avail since our best hope lies not in compulsion but in voluntary effort.

Such a sentiment already generally exists to a large extent with respect to incest, and the marriage of persons as noticeably defective as idiots or those afflicted with insanity, and also in America with respect to miscegenation, but a cautious and intelligent examination of the more obscure defective traits, exhibited in the somatoplasms of the various members of families in question, is largely an ideal of the future. Under existing conditions non-eugenic considerations such as wealth, social position, etc., often enter into the preliminary negotiations of a marriage alliance, but an equally unromantic caution with reference to the physical, moral, and mental characters that make up the biological heritage of contracting parties is less usual.

The scientific attitude is not necessarily opposed to the romantic way of looking at things. If the bandage across the eyes of blind Cupid is allowed to slip a little in so important and far-reaching an operation as "falling in love" it is perhaps just as well. The dialogue in "Two Gentlemen of Verona" between Julia and Lucetta is quite to the point where the eager and curious Julia says to her maid,—

> "But say, Lucetta, now we are alone,
> Woulds't thou counsel me to fall in love?"

and the canny Lucetta makes reply,—

"Aye, Madam, so you *stumble not unheedfully.*"

This advice is simply "organized common sense," and romance, which dispenses with this balance-wheel, although it may be entertaining and always exciting at first, is sure to be disappointing in the end. Marriages may be "made in heaven," but, as a matter of fact, children are born and have to be brought up on earth, and there is nothing particularly romantic in defective children who might better never have been born. It follows without saying that it will be much easier to stamp out bad germplasm when an educated sentiment becomes common among all people everywhere.

D. SEGREGATION OF DEFECTIVES

Persons with hereditary defects, such as epileptics, idiots, and certain criminals, who become wards of the state, should be segregated or confined in comfort so that their germplasm may not escape to furnish additional burdens upon society. "We have become so used to crime, disease and degeneracy that we take them for necessary evils. That they were, in the world's ignorance, is granted. That they must remain so, is denied" (Davenport).

"The great horde of defectives once in the world have the right to live and enjoy as best they may whatever freedom is compatible with the lives and freedom of other members of society," says Kellicott, "but society has a right to protect itself against repetitions of hereditary blunders."

There is one grave danger connected with the administration of our humane and commendable philanthropies for the unfortunate, since it frequently happens that defectives are kept in institutions until they are sexually mature or are partly self-supporting, when they are liberated only to add to the burden of society by reproducing their like.

Furthermore, if defectives of the same sort are collected together in the same institutions, unless sexual segregation is strictly maintained, they may by the very circumstance of proximity tend to reproduce their kind just as defectives in any isolated community tend to multiply. There is much misplaced philanthropy that is euthenic but not eugenic. The temporary troubles of the individual may be alleviated only to make possible a future addition to the burden of society.

David Starr Jordan cites the interesting case of *cretinism* which occurs in the valley of Aosta in northern Italy, to prove the wisdom of the sexual segregation of defectives. Cretinism is an hereditary defect connected with an abnormal development of the thyroid gland which results in a peculiar form of idiocy usually associated with goitre.

"In the city of Aosta the goitrous *cretin* has been for centuries an object of charity. The idiot has received generous support, while the poor farmer or laborer with brains and no goitre has had the severest of struggles. In the competition of life a premium has thus been placed on imbecility and disease. The *cretin* has mated with *cretin*, the goitre with goitre,

and charity and religion have presided over the union. The result is that idiocy is multiplied and intensified. The *cretin* of Aosta has been developed as a new species of man. In fair weather the roads about the city are lined with these awful paupers—human beings with less intelligence than a goose, with less decency than the pig."

Whymper, writing in 1880, further observes: "It is strange that self-interest does not lead the natives of Aosta to place their *cretins* under such restrictions as would prevent their illicit intercourse; and it is still more surprising to find the Catholic Church actually legalizing their marriage. There is something horribly grotesque in the idea of solemnizing the union of a brace of idiots, and, since it is well known that the disease is hereditary and develops in successive generations the fact that such marriages are sanctioned is scandalous and infamous."

Since 1890 the *cretins* have been sexually segregated, and in 1910 Jordan reported that they were nearly all gone.

E. DRASTIC MEASURES

A fifth method of restricting undesirable germplasm in the case of confirmed criminals, idiots, imbeciles, and rapists may be mentioned, namely, the extreme treatment of either asexualization or vasectomy. The latter is a minor operation confined to the male which occupies only a few moments and requires at most only the application of a local anæsthetic, such as cocaine. There are probably no disturbing or even inconvenient

after effects from this operation. It consists in removing a small section of each sperm duct and is entirely effectual in preventing subsequent parenthood.

In the female the corresponding operation, which consists in removing a portion of each Fallopian tube, is much more severe, but not impracticable or dangerous.

According to Laughlin who has carefully collected data on the subject, in ten of the fifteen states which have enacted eugenical sterilization statutes the law is still (1921) on the statute books, unattacked by courts and so still available for use. From the beginning of legal sterilization in the United States in 1907 until January 1st, 1921, a total of 3233 cacogenic persons have been made sexually sterile under the several statutes.

Laughlin goes on to point out that "the nature of administrative machinery, which will work and which will fail, is, from the experiments already made, fairly well known, so that if the principle of eugenical sterilization has public support, practically any state legislature can, if it chooses, enact a well-functioning law."

The possibility of the abuse of sterilization if legalized is, however, so great that this extreme method of last resort will be for a long time doubtless of very questionable application.

6. The Conservation of Desirable Germplasm

The eugenic ideal may be approached not only negatively by the restriction of undesirable germplasm, but

also positively by the conservation of desirable germplasm.

The various ways in which this improvement of society may be brought about are:

A. BY ENLARGING INDIVIDUAL OPPORTUNITY

Much good human germplasm goes to waste through ineffectiveness on account of unfavorable environment or lack of a suitable opportunity to develop.

Every agency which contributes toward increasing the opportunity of the individual to attain to a better development of his latent possibilities is in harmony with a thoroughly positive eugenic practice. Thus better schools, better homes, better living conditions, in short, all euthenic endeavor, directly serves the eugenic ideal by making the best out of whatever germinal equipment is present in man.

B. BY PREVENTING GERMINAL WASTE

Much good protoplasm fails to find expression in the form of offspring because one or the other of possible parents is cut off either by preventable death or by social hindrances. To avoid such calamities is a part of the positive program of eugenics.

a. Preventable Death

War, from the eugenic point of view, is the height of folly, since presumably the brave and the physically fit march away to fight, while in general the unqualified

stay at home to reproduce the next generation. When a soldier dies on the battlefield or in the hospital, it is not alone a brave man who is cut off, but it is the termination of a probably desirable strain of germplasm.

David Starr Jordan has presented this matter very clearly. He points out that the "man with a hoe" among the European peasantry is not the result of centuries of oppression, as he has been pictured, but rather the dull progeny resulting from generations of the unfit who were left behind when the fit went off to war never to return.

Benjamin Franklin, with characteristic wisdom, sums up the situation in the following epigram: "Wars are not paid for in war time; the bill comes later."

b. Social Hindrances

There are many conditions of modern society which act non-eugenically.

For instance, the increasing demands of professional life prolong the period necessary for preparation, which, with the "cost of high living," tends toward late marriage. In this way much of the best germplasm is very often withheld from circulation until it is too late to be effective in providing for the succeeding generation.

Certain occupations such as school-teaching and nursing by women are filled by the best blood obtainable, yet this blood is denied a direct part in molding posterity, since marriage is frequently either forbidden or

regarded as a serious handicap in such lines of work. Advertisements concerning "unincumbered help" and "childless apartments" tell their own deplorable tale.

One of the darkest features of the dark ages from a eugenic standpoint was the enforced celibacy of the priesthood, since this resulted, as a rule, in withdrawing into monasteries and nunneries much of the best blood of the times, and this uneugenic custom still obtains in many quarters to-day.

C. BY SUBSIDIZING THE FIT

It is possible that if some of the philanthropic endeavor now directed toward alleviating the condition of the unfit should be directed to *enlarging the opportunity of the fit*, greater good would result in the end. In breeding animals and plants the most notable advances have been made by isolating and developing the best, rather than by attempting to raise the standard of mediocrity through the elimination of the worst.

One leader is worth a score of followers in any community, and the science of genetics surely gives to educators the hint that it is wiser to cultivate the exceptional pupil who is often left to take care of himself than to expend all the energies of the instructor in forcing the indifferent or ordinary one up to a passing standard. The campaign for human betterment in the long run *must do more than avoid mistakes.* It must become aggressive and take advantage of those human mutations or combinations of traits which appear in the exceptionally endowed.

7. Who shall sit in Judgment?

In the practical application of a program of eugenics there are many difficulties, for who is qualified to sit in judgment and separate the fit from the unfit?

There are certain strongly marked characteristics in mankind which are plainly good or bad, but the principle of the independence of unit characters demonstrates that no person is wholly good or wholly bad. Shall we then throw away the whole bundle of sticks because it contains a few poor or crooked ones? Is it wise to burn the barn in order to kill the rats?

The list of weakling babies, for instance, who were apparently physically unfit and hardly worth raising upon first judgment, but who afterwards became powerful factors in the world's progress, is a notable one and includes the names of Calvin, Newton, Heine, Voltaire, Herbert Spencer and Robert Louis Stevenson.

Dr. C. V. Chapin recently said with reference to the eugenic regulation of marriage by physician's certificate: "The causes of heredity are many and very conflicting. The subject is a difficult one, and I for one would hesitate to say, in a great many cases where I have a pretty good knowledge of the family, where marriage would, or would not, be desirable."

Desirability and undesirability must always be regarded as relative terms more or less undefinable. In attempting to define them, it makes a great difference whether the interested party holds to a puritan or a cavalier standard. To show how far human judgment may err as well as ho[illegible] ion

changes, there were in England, as recently as 1819, 233 crimes punishable by death according to law.

One needs only to recall the days of the Spanish Inquisition or of the Salem witchcraft persecution to realize what fearful blunders human judgment is capable of, but it is unlikely that the world will ever see another great religious inquisition, or that in applying to man the newly found laws of heredity there will ever be undertaken an equally deplorable eugenic inquisition.

It is quite apparent, finally, that although great caution and broadness of vision must be exercised in bringing about the fulfillment of the highest eugenic ideals, nevertheless in this direction lies the future path of human achievement.

8. Eugenics, not "Bluegenics"

Eugenics has been called the "dismal science" by romantic people who chafe under the restrictions of common sense, and by conscientious individuals who are depressed by the appalling hereditary blunders made by mankind, but, as a matter of fact, eugenics presents the brightest hope for the future of humanity. Some of the unattractiveness of the eugenical program lies in the fact that it calls for results in the distant future in which there can be little or no personal participation, and often at the expense of present day comforts. It is a lofty ideal of altruism and patriotism, and in the words of Major Leonard Darwin, "*an ideal to be followed like a flag in battle without thought*

9. The Moral

Race-preservation, not self-preservation is the first law of nature. Because the laws of heredity work relentlessly within predetermined limits is no reason for branding eugenics with the mark of a fatalistic philosophy that would avoid personal responsibility. The Florida orange-grower who uses his intelligence and plants frost-resisting varieties to replace those overtaken by frost does not blame fate for his losses. It is never fatalistic to seek to find out the true determining causes of a disaster and to apply the obvious remedy. As Osborn has said:—"To know the worst as well as the best in heredity; to preserve and select the best,—these are the most essential forces in the future evolution of human society."

Our hereditary endowment may be something given us without our consent and connivance and the accident of our birth may determine very largely the environment in which we must work out our salvation but *there lies a sleeping giant of possibility in everyone*, and, whether we have one talent or five or ten, the individual response we make is our own and we alone are responsible for it.

Finally, to quote the wise words of Huxley,— "To learn what is true in order to do what is right is the summing up of the whole duty of man, for all who are not able to satisfy their mental hunger with the east wind of authority."

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